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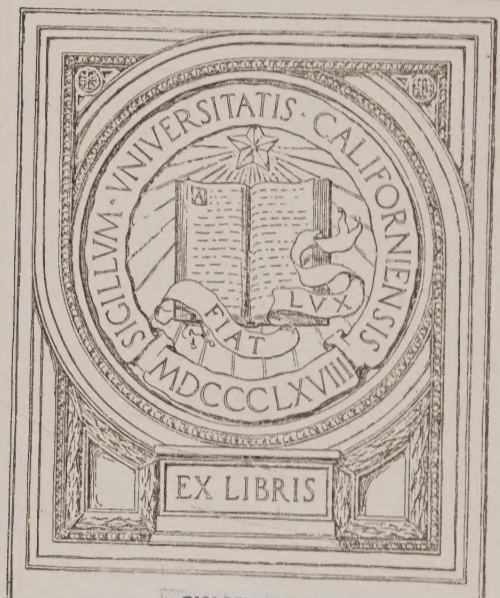

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BIOLOGICAL MONOGRAPHS AND MANUALS

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No. VII

The Composition and Distribution of the Protozoan Fauna of the Soil

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The Composition and Distribution of the Protozoan Fauna of the Soil

BY

H. SANDON, M.A.

General Microbiology Department, Rothamsted Experimental Station

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EDITORS' PREFACE

THE increasing specialisation in biological inquiry has made it impossible for any one author to deal adequately with current advances in knowledge. It has become a matter of considerable difficulty for a research student to gain a correct idea of the present state of knowledge of a subject in which he himself is interested. To meet this situation the text-book is being supplemented by the monograph.

The aim of the present series is to provide authoritative accounts of what has been done in some of the diverse branches of biological investigation, and at the same time to give to those who have contributed notably to the development of a particular field of inquiry an opportunity of presenting the results of their researches, scattered throughout the scientific journals, in a more extended form, showing their relation to what has already been done and to problems that remain to be solved.

The present generation is witnessing "a return to the practice of older days when animal physiology

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was not yet divorced from morphology." Conspicuous progress is now being seen in the field of general physiology, of experimental biology, and in the application of biological principles to economic problems. In this series, therefore, it is intended that biological research, both pure and applied, shall be represented.

F. A. E. C
D. W. C.

PREFACE

During the early years of the investigation of any group of soil organisms a considerable part of the work is necessarily devoted to the identification of the forms comprised in the group, and to determining whether they are of general or merely of local occurrence. The present volume was originally planned simply as an account of one more such investigation, differing from others that have been published only in being based on the examination of a larger and more varied collection of soils than most of the other investigators have used. On second thoughts, however, it seemed that the time had come when this chapter of soil protozoology could be brought to a close by bringing together all the available records, reconciling wherever possible their mutual inconsistencies and contradictions, and thus presenting for the use of the soil microbiologist and the general naturalist a clear and tolerably complete picture of this group of organisms and of their distribution in the soil.

In saying this I am making no claim to finality for the present volume. The soil undoubtedly harbours some protozoa at present unidentified and possibly quite new to science. Many of the genera and species here recorded are very imperfectly known, and more complete knowledge of their morphologies

and life-histories may necessitate considerable modifications in the nomenclature and classification that have been adopted. Also a reading of the section dealing with the ecological aspect of the subject will make it abundantly clear how rudimentary our present knowledge of this part of the subject is. But while future work will inevitably amplify and correct much of the detail, it seems very unlikely that the main outlines of the picture given here will require any considerable alteration. The monograph is therefore being published in the belief that it will be of use to all who desire information about this important part of the soil fauna.

No attempt is made here to survey the whole field of soil protozoology, as this will be done in other volumes at present in course of preparation—namely, *Soil Protozoa*, by D. W. Cutler and L. M. Crump (Rothamsted Monographs), and *Problems in the Physiology of the Protozoa*, by D. W. Cutler, in this series. An account of the modern technique will appear shortly in the section of Soil Protozoa in the new edition of Abderhalden's *Handbuch der Biologischen Arbeitsmethoden.*

Though the greater part of the manuscript of this volume was completed while I was working at Rothamsted (where all the original work on which it is based was done), the decision to publish it in its present form was only made after I had already left for a temporary residence in America. In obtaining the additional illustrations which this decision made desirable, I have been greatly helped by Professor

Calkins, of Columbia University, who not only obtained for me the admirable services of Miss R. Bowling, but himself undertook the whole supervision of the preparation of the drawings. It is a pleasure to be able to thank him publicly for his help, which is but typical of the generous hospitality with which the visitor to that country is welcomed.

The circumstances of its publication have thrown the whole of the work of seeing the book through the press on to Mr D. W. Cutler, and has consequently added still further to my indebtedness to him for his great help throughout the work—help that has not been confined to advice and encouragement, but included much laborious work in the examination of cultures when it became apparent that the task of examining all the soils would be too prolonged if undertaken single-handed.

My thanks are also due to my brother, Frank Sandon, for help in the statistical treatment of the data; to Professor S. A. Waksman for suggesting several improvements in the manuscript; and to all the colleagues in many lands through whose kindness it was possible to obtain such a large and varied collection of soil samples for examination.

Rothamsted Experimental Station,
Harpenden.

FOREWORD

At a joint session of the sections of Zoology and Agriculture of the Sheffield meeting of the British Association in September 1910, Dr (now Sir John) Russell and Dr H. B. Hutchinson gave an account of their observations on the results following partial sterilisation of the soil, and added some remarks on the presence and possible influence of protozoa on the fertility of the soil. In the subsequent discussion the paucity of knowledge on the species and bionomics of the protozoa present in the soil was strikingly revealed, and it was clear that on the information available the inter-relations of the community of organisms in the soil could be considered only in the most general terms and that far too much had necessarily to be left to speculation. Suggestions were advanced to account for some of the observed facts reported by Drs Russell and Hutchinson, and the value of cultural methods for the investigation of soil protozoa was emphasised, but there was not, and there could not then have been, an adequate discussion on the protozoa of the soil or on their significance.

The first pre-requisite to a consideration of the problems involved was obviously to ascertain as completely and accurately as possible the species of micro-organisms present in soils of various qualities from different localities. The great progress

made by such investigations upon the soil protozoa will be realised by reference to the present monograph. New forms doubtless remain to be discovered in the soil, the nomenclature of some of the species already known will be amended, and it is admitted that the structure and life-history of many known species — even of some of the common species— have been only imperfectly investigated; nevertheless the author is justified in his statement that the main outlines of the taxonomic work are not likely to undergo any considerable alteration. By means of the keys and other data provided it should not be difficult for future workers to recognise most of the two hundred and fifty species of protozoa which have been recorded from the soil. A plea may be interpolated here for precision in identification of the organism on which any work of importance is to be based; not only the genus but the species should be determined so as to permit subsequent workers to repeat and perhaps to extend any given series of observations. Now that methods for the culture of the protozoa of the soil are so well established, the difficulty of obtaining the organisms in sufficient number or in suitable condition for precise determination is greatly diminished, and with the aids given in this volume the diagnosis should in most cases be a comparatively simple matter. The systematic side of soil protozoology may therefore be regarded as being in a satisfactory position.

Investigations which followed upon those of Russell and Hutchinson have shown that there is

an intimate inter-relationship between the protozoa and the bacteria of the soil and that the protozoa must be regarded as an important part of the general soil population. Knowledge of the physiology of the soil protozoa and of their ecology is, however, admittedly almost rudimentary. Though food supply is the main factor in influencing distribution and abundance, little is known of the food requirements, either qualitative or quantitative, of even the common species. Investigations on these lines and on life-histories are much needed.

Though the protozoa of the soil have been the subject of investigation by Ehrenberg, Greef, Beijerinck, and others, the work of Russell and Hutchinson at Rothamsted in 1909 may justly be regarded as having given the stimulus to modern researches in soil protozoology. The later investigations, in which Sir John Russell has throughout maintained a keen interest, carried on by Goodey, Martin, Lewin, Cutler, Crump, and Sandon at Rothamsted, have demonstrated the complexity and importance of the problems in which the soil protozoa are involved. It is therefore especially appropriate that the present monograph should be issued from the General Microbiology Department of the Rothamsted Experimental Station. That it will be welcomed by all who are interested in the biology of the soil is certain.

J. H. ASHWORTH.

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The Composition and Distribution of the Protozoan Fauna of the Soil

INTRODUCTION

Although the occurrence of protozoa in soils has been well known since the work of Ehrenberg nearly a century ago, serious interest in them can only be regarded as having commenced with the publication by Russell and Hutchinson, in 1909, of their theory of partial sterilisation. Without discussing that theory in detail, it is enough to say that attention was drawn to the protozoa primarily as devourers of bacteria, it being supposed that their phagocytic action was sufficiently extensive seriously to restrict the bacterial processes going on in the soil. The earlier objections based on the belief that the protozoa were present in the soil merely as stragglers brought in accidentally from other more natural habitats, existing for the greater part of the time only as inert cysts and incapable of taking any active part in the life of the soil community, have now been entirely removed by the demonstration that, at any rate in the soils of temperate climates, they are present at all times of the year, leading an active life, often attaining very high numbers, and undoubtedly constituting an important component of the soil population. As to

the rôle played by them in the soil economy, however, it must be confessed that the work of these seventeen years has yielded disappointingly little really convincing information, and in view of the very wide diversity of forms occurring in the soil it seems very probable that this failure may be, in part at any rate, due to an over-simplification of the problem by the assumption that they can all be considered together as leading very similar lives, or that at the most they need only be divided into the main classes of ciliates, amœbæ, and flagellates.

If, however, we turn from the pure soil investigations to work that has been going on in other directions, we find good ground for the belief that future progress in this subject will be less a matter of generalisations about the protozoa as a whole, and more a question of accurate studies of the lives of individual species; and similarly that their influence on the bacteria may be limited to certain groups rather than to affecting the whole bacterial flora indifferently. As long ago as 1897, Frosch[45] found that a certain amœba isolated from the soil fed much more readily on some soil bacteria than on others. Unfortunately Frosch was not interested particularly in soil processes, and consequently did not identify the bacteria. The amœba was called by him *A. nitrophila*, Beijerinck, but from his brief description it seems undoubtedly to have been *Nægleria gruberi* (Schardinger) Wilson, one of the commonest of all soil protozoa. Similar observations have been made since then by a number of investigators. Thus Oehler[87] showed that some

limax amœbæ have distinct preferences between Gram positive and Gram negative bacteria and between old and young cultures of them—preferences which are not shown by some larger amœbæ. More recently Sewertzeff[110] has stated that the soil amœbæ feed most readily on the micrococci and bacteria, less readily on the bacilli, and not at all on the fungi, yeasts, and actinomycetes, and a series of papers by Schaeffer[102-106], while dealing with amœbæ not common in soils, are of great interest as showing how complex the selection of food may become. For the flagellates we have Alexeieff's evidence[4] that two nearly-related species of *Cercomonas* feed on different types of bacteria, the one selecting an organism which he calls *Bacillus mitochondrialis*, while the other feeds on cocci and small bacteria. Müller[82] has also claimed that the flagellates involved in the self-purification of water ingest the pathogenic bacteria in preference to the true water bacteria. In the case of the ciliates Hargitt and Fray[55] and Phillips[92] found that even *Paramœcum*, which ingests all solid particles indifferently, cannot obtain nourishment from all bacteria, and Cutler and Crump[25] have similarly demonstrated the inability of *Colpidium* to develop on a diet of *Sarcina lutea*.

The object of the present work is therefore to pave the way for more detailed inquiries of this kind by giving a general review of the forms of protozoa occurring in the soil, and of the factors influencing their distribution. It is based primarily on the examination carried out at Rothamsted of 148 soil

samples obtained from many widely separated parts of the world and representing many different soil types. Other investigators have published lists of the protozoa found in soil in the course of their own work; but unfortunately most of them have been soil scientists without any special training in systematic protozoology to whom the great labour involved in mastering such a subject would have been pure waste of time, and consequently their identifications are often of uncertain value. Such records have been compared as critically as possible with our own findings, and there seems no reason to doubt that the results as recorded here give in the main an accurate and practically complete picture of the forms with which the soil microbiologist is concerned. The earlier part of the present volume is therefore devoted to giving such a general picture of the protozoal fauna of the soil, followed by an analysis of the factors influencing its distribution. Brief notes on the soils from which the new data employed were obtained are added. In the second part will be found short descriptions of all the species so far authentically recorded from soils, together with figures of the more important ones, and some original observations in the case of new species or of those of which the existing descriptions appear inadequate. Artificial keys are added to assist identification except in the case of the naked Rhizopoda, which do not lend themselves to this treatment. It is hoped that this treatment will enable the soil biologist to identify the forms with which he is dealing without

the necessity of referring to the scattered and often rather inaccessible literature which is at present required for that purpose. And while probably the nomenclature and classifications employed are not entirely free from objections, it is further hoped that they will lead to greater uniformity and to the avoidance of some of the ambiguities which detract considerably from the value of much of the past work.

Methods.

Direct examination of soil with a microscope gives very little idea of the wealth of life with which it teems, and investigators (such as Francé[44]) who have employed this method for seeking protozoa have found little except shells of the testaceous rhizopods and an occasional ciliate. The only practicable method consists in inoculating the soil to be examined into a suitable culture medium and then examining the culture from time to time to find what protozoa develop. The objection may be raised that some of the forms are so adapted to life in the soil that they are not capable of developing in the artificial conditions of such cultures, but the ingenious methods by which Martin and Lewin[79] obtained active protozoa direct from the soil itself yielded only forms which can also be found by the cultural method. We are therefore justified in assuming that the latter is quite adequate. The testaceous rhizopods, however, multiply very slowly in cultures, and as they can be detected by direct examination of the soil, this is the most satisfactory way of seeking them.

Although protozoa will develop on any of the media commonly used in soil bacteriology either liquid or solid (provided they are not allowed to become too dry), yet all such media are not equally suitable. Cunningham and Löhnis[24] have given some valuable data as to the development of protozoa in various bacteriological media inoculated with soils. Yakimoff and Zérèn[126] have also described at some length the different results obtained with soil cultures in various media such as vegetable infusions of several kinds, horse-dung infusion, soil extract, and dilute bouillon, with respect both to the species developing and to the rate at which they develop. They found that while some species (e.g., *Colpoda steinii* and *Monas guttula*) grew well in practically all the media employed, others appeared in only one or two of them. From the way in which their data are presented, however, it is impossible to ascertain whether these differences were constantly observed or were merely accidental.

The media used in the present work were nutrient agar, dilute hay infusion, and sterile tap water, and the cultures were examined weekly for four weeks. For the last 107 soils examined the results given were obtained from cultures in all these three media, but unfortunately with the earlier examples examined before the idea of extending the inquiry to its present scale had been adopted, either the water or both the water and the hay infusion cultures were omitted. The effect of these omissions can be seen from Table I., in which the

results obtained from the soils for which the complete series of cultures were made are analysed.

TABLE I.

Media used.	Numbers of Species found per Sample (Averages of 107 Samples).				
	Flagellates.	Ciliates.	Amœbæ, etc.*	Testaceous Rhizopods.	Total Protozoa.
Agar . . .	4·55	1·0	1·6	0·55	7·7
Agar and hay infusion	6·7	2·6	2·2	1·2	12·7
Agar, hay infusion and water	7·2	3·4	2·45	2·0	15·05

* Throughout the tables this term is used to cover, in addition to the true amœbæ, all the other naked rhizopods (e.g., *Nuclearia*) and the heliozoa (which were only very occasionally found).

Consequently for the quantitative comparison of the results from all the soils, the numbers of species obtained from those for which the complete series of cultures was not used have been multiplied by the following factor :—

	Flagellates.	Ciliates.	Amœbæ, etc.	Testaceous Rhizopods.
Agar alone . . .	1·6	3·3	1·5	3·6
Agar and hay infusion .	1·1	1·3	1·1	1·70

Although four weeks is long enough for the development of most of the flagellates, ciliates, and amœbæ to take place, there are some (e.g., *Euglena* and *Polytoma*) which develop very slowly, and it is probable that if cultures had been kept longer such

forms would have been found more frequently. In cases where incubation was extended for an additional week or more, however, the additional records resulting were too few to justify the general adoption of this plan.

Examination of the Cultures.—In general it is much more satisfactory when working with mixed cultures to identify live protozoa than dead ones. One great objection to the use of stained preparations for identification is that in the course of fixation and staining a large number of the organisms are lost, so that only those forms developing most strongly in the cultures are found in the final preparation. Also many organisms have characteristic movements or attitudes which are sometimes useful aids to rapid identification. Structures such as the contractile vacuole can generally only be observed in living specimens, and flagella and cilia can often be detected more readily when they are moving than when they are quite motionless.

To examine the cultures, therefore, a little of the liquid is taken up with a loop of platinum or chrome wire, spread out on a slide and covered with a coverslip, and then examined immediately under the microscope. Often, however, the movements of the animals are too rapid and it becomes necessary to reduce them. For this purpose there is unfortunately no single method that is generally applicable, and consequently it is usually necessary to try several before one is found suitable for the organism under examination. Sometimes the

asphyxiation produced by remaining under the coverslip for a few minutes is sufficient. Other species can be quieted down by brief exposure to dilute osmic acid vapour or by use of a narcotic such as cocaine. Tannic acid in dilute solution (0.4 per cent.) sometimes produces the same effect, and when it is applicable has the further merit of producing slight swelling of flagella and cilia. To kill flagellates without distortion a dilute solution of copper sulphate (0.5 per cent. to 1.0 per cent.) may be employed, while a solution of iodine in potassium iodide is often very valuable as it stains the organisms at the same time as killing them. Acetic carmine generally results in considerable shrinking and distortion, but is sometimes useful for demonstrating the positions and number of the nuclei (especially in ciliates). The vital stains (neutral red, methylene blue) can be used but the results are generally disappointing.

For permanent preparations of all but the largest ciliates, thin films can be made on coverslips, which after fixation can be handled easily. Schaudinn's alcoholic corrosive sublimate + 5 per cent. acetic acid, and Bouin's picric acid-formalin solution are the most generally useful fixatives; while as stains, borax carmine and Heidenhain's hæmatoxylin will be found to serve most purposes. Instructions for the preparation and use of these can be found in most biological laboratory manuals.

Effect of Storage of Soil Samples.—From the figures corrected in the manner just described the effect of storage of soils on the number of species

found was tested. Some of the samples had been kept for periods of anything up to $3\frac{3}{4}$ years before opportunity was found for examining them, and consequently, had storage been detrimental, the records obtained would have been incomplete, and the comparison of soils stored for different periods would have been impossible. Fortunately, however, though the older samples seem to show a slight falling off in the number of species found, the figures as a whole

TABLE II.

Length of Storage.	No. of Cases.	Average Number of Species of				
		Flagellates.	Ciliates.	Amœbæ.	Testaceous Rhizopods.	Total Protozoa.
Soil quite fresh	7	8·0	4·0	2·4	3·4	17·8
0 to 1 month .	4	6·6	3·8	2·3	3·9	16·6
1 „ 6 „ .	61	6·5	3·7	2·9	2·0	15·1
6 „ 12 „ .	23	9·6	5·9	3·5	3·4	22·4
1 „ 2 years .	12	7·2	3·0	2·9	0·9	14·0
over 2 „ .	41	6·2	2·9	1·4	1·0	11·5

indicate that this effect is of little importance (Table II.).

It is possible, however, that the complete absence from the present records of some of the forms, such as *Paramœcium*, which have frequently been recorded from soils by other observers, may be due to the use of stored instead of fresh soils. This suggestion is particularly plausible in the case of *Paramœcium* as the common species of this genus have never been known to form resistant cysts.

Personal Factors.

Owing to the amount of labour involved in examining the cultures, Mr D. Ward Cutler very kindly assisted throughout the latter part of the work. The plan then adopted was for duplicate cultures to be made in each of the three media, and for each of us to examine one set of the duplicates. In all, 87 samples were examined jointly in this way, the remaining 61 being examined by myself alone.

There is no indication that personal factors (increasing experience, or the examination of the duplicate cultures by different observers instead of by a single person) materially affected the results, though those obtained from some of the soils examined during the first few months may be a little defective owing to lack of familiarity with some of the forms encountered.

Descriptions of Soils Examined.

Descriptions of some of the soils used in this investigation and of the protozoa found in them have already been published,[100, 101] and consequently, although the results obtained from them will be incorporated in the later statistical part of this paper, there is no need to repeat them in detail here. The soils in question were Spitsbergen (43-50),* and those collected by the Quest Expedition from Elephant Island (19), South Georgia (13-18), Tristan da Cunha (20-25), Gough

* The figures given in brackets are the reference numbers of the soils.

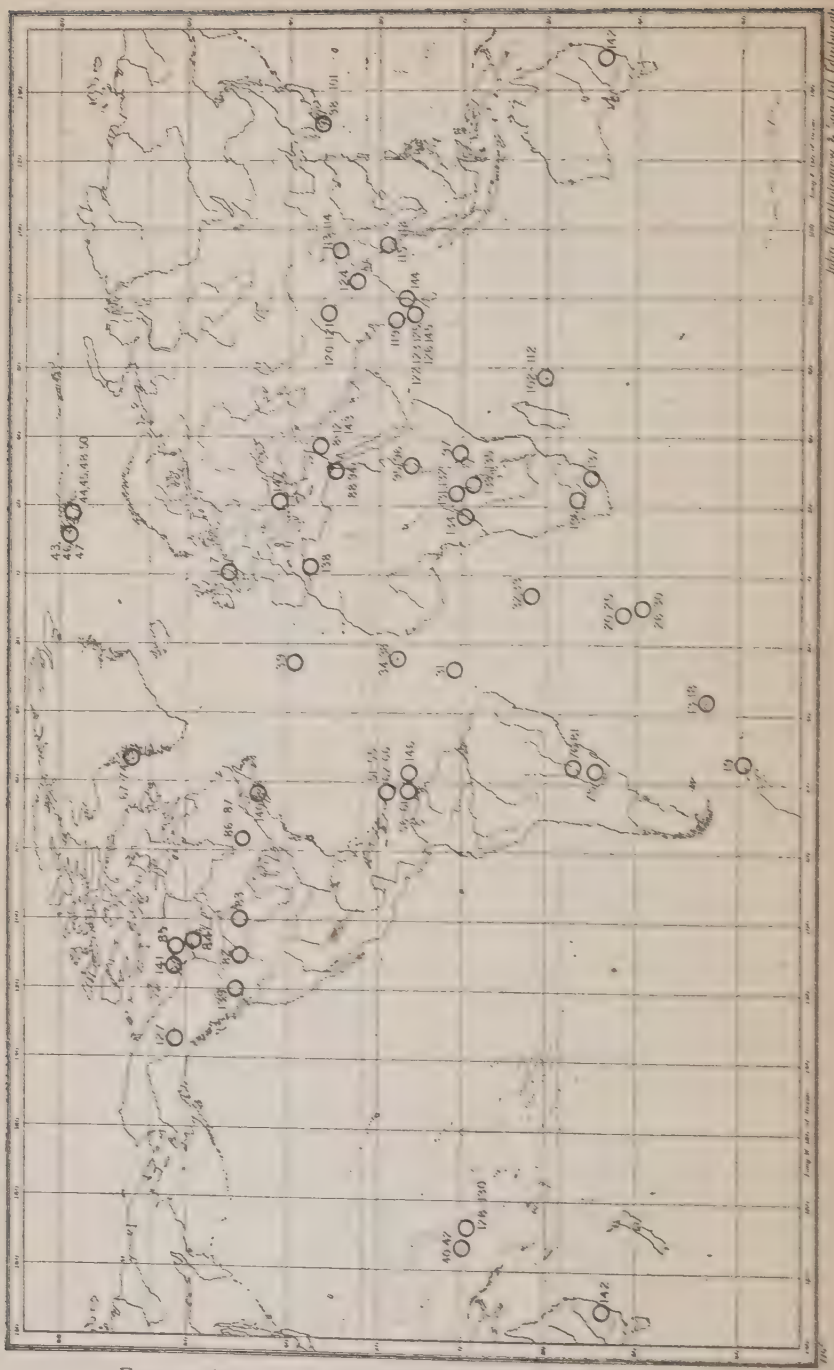

FIG. 1.—Map of World showing origins of soils examined.

Island (26-30), St Paul's Rocks (31), St Helena (32, 33), St Vincent (Cape Verde Islands) (34-38), and San Miguel (Azores) (39). Only one soil from Continental Europe and none from U.S.A. were examined, as some work has already been done on soils from these regions, and there is every prospect of the work being extended by investigators who will have the advantage of using fresh material and of knowing intimately the ecological conditions of the soils in question.

The species of protozoa found in the various soil samples are given in Charts 1, 2, and 3.

Arctic Soils. *Greenland.*—Samples 67, 68, 69, 70, 71, 72, 73A, 73B, 74. These soils were all collected in the neighbourhood of the Danish Arctic Station at Disko (lat. 69° N.) by Dr Morten Porsild.

(67). A coarse soil from a plain which is usually damp, but was dry at the time of sampling. Vegetation: *Eriophorum Scheuchzeri, Carex rigida, Salix herbacea, S. groenlandica, Empetrum,* green and blue algæ, and mosses.

(68). A similar soil with little organic matter taken from a higher, more exposed, and drier spot. It supported a very poor heath of *Myrtillus uliginosa, Empetrum, Carex rigida,* and lichens.

(69). A black, peaty soil containing some mineral matter. Vegetation: *Empetrum, Hypnum, Hylocomium,* etc.

(70). This sample was taken from the same spot as the sample No. 7 taken by Wulft and used by Barthel[7] in his bacteriological investigations. He

found that it contained no Azotobacter and that there was no nitrification, but that ammonification and butyric fermentation were strong. The soil was a layer of partly decomposed leaves and supported a varied herbaceous growth.

(71). A well-humified basaltic soil also with a varied herbaceous flora (*Salix herbacea*, *Poa alpina*, *Polygonum viviparum*, etc.).

(72). A rather peaty soil from a poor heath developing on basaltic gravel. It is interesting to note that more protozoa were found in this than in the soils on which the growth was more luxuriant.

(73A and 73B). Taken near the surface and at a depth of 45 cms. respectively from a luxuriant heath on basaltic soil. Vegetation: *Cassiope tetragona*, *Salix glauca*, *Equisetum arvense*, etc.

(74). A garden soil enriched every year with poultry manure. Whereas most of the Greenland soils were rather poor in protozoa this one was richer than any other examined in the whole course of the work, yielding 46 species. Consequently the extreme climate of this arctic land is not in itself an obstacle to the plentiful development of protozoa provided that the soil is rich and in good condition. No doubt the abundant manuring was responsible for the great numbers found in this soil.

Other arctic and antarctic soils examined were those from Spitsbergen, Elephant Island, and South Georgia. The last, though not actually within the Antarctic Circle, is grouped with these in Table II. as it is within the limits of the southern pack ice. The

results obtained from these soils are published in previous papers.[100, 101]

Temperate Soils.—These fall into two groups, viz., the Oceanic Islands (Tristan da Cunha, Gough Island, and Azores) already described,[101] and those from regions where the conditions are more continental, viz., England, Serbia, Canada, Japan, and Australia.

England. — The Rothamsted soils have been omitted from the statistical part of this survey, as the more extensive and detailed investigations to which they have been submitted do not permit their comparison with the others. The remaining soils were examined for various reasons and are not taken as typical English soils.

(1 and 2). Light, sandy soils from experimental plots 2A and 8B from Stackyard Field, Woburn. These plots have received annual dressings of ammonium sulphate for nearly forty years, and as a result are very acid, and the crops are complete failures.

(3). A sample from waste gravel land at No-Man's-Land near Harpenden.

(4). An arable field near Harpenden where the soil was light grey in colour owing to an outcrop of chalk.

(5). Sand dunes at Blakeney, on the Norfolk coast. Vegetation: marram grass.

(6). Slightly older moss-covered dunes at the same place.

(7). Mud from the salt marshes at Blakeney.

Canada.—Through the kindness of Dr F. T. Shutt a large variety of Canadian soils were received. Unfortunately, it was only possible to examine the following ten, which were selected as giving as wide a range of types and of localities as possible.

(82 and 83). Virgin prairie soils from Lethbridge (South Alberta) and Brandon (Manitoba) respectively.

(84). Arable, dunged soil from Fort Smith in the North-West Territory (lat. 60° N.).

(85 and 141). Virgin soils from the North-West Territory, from Fort Resolution on the southern shore of Great Slave Lake and from Mission Providence on the Mackenzie River respectively. Samples 84 and 141 were both deficient in humus, and the number of protozoa found was correspondingly low; and 85 was a coarser soil containing more humus, and the number of protozoa was up to the average.

(86 and 87). Unmanured pasture and woodland soils from the Ottawa Experimental Farm.

(127). A fine grey virgin soil from Swede Creek, Yukon Territory. This sample had set into a hard brick in the tin in which it was stored, and yielded only two species of protozoa.

(139). Unmanured virgin soil from the neighbourhood of the Experiment Station at Invermere, British Columbia.

(140). Woodland soil from the city reservoir at Charlottetown, Prince Edward Island.

All the Canadian soils were rather poor in protozoa, possibly as a result of the rather prolonged

storage to which they had been submitted before examination.

Japan.—The four soils 98 to 101 all came from the Fukuoka University Farm, being taken respectively from a virgin pinewood, a dry upland field of cabbages, an irrigated field where rice had been grown for centuries without rotation, and a dry mulberry field. In spite of having been air-dried before being put into the tins in which they were stored for $1\frac{1}{2}$ years the yield of protozoa was good, the irrigated rice soil being the poorest in this respect.

Serbia.—Sample 147 was a rich, deep, meadow soil, slightly alkaline in reaction, from Topchida, near Belgrade.

Australia.—It was only possible to examine a single Australian soil, No. 142. This was a tenacious, black, clayey soil from the northern part of the wheat belt of New South Wales. It was a basaltic alluvial or drift soil, alkaline in reaction, and came from an inland locality where the annual rainfall is about 19 in. and very erratic.

Tropical and Sub-Tropical Islands.

Nauru and Ocean Island.—These are small islands situated near to one another in the Pacific Ocean and practically on the Equator. Both have large phosphatic deposits derived from guano. Three samples from each were examined which were all deep black in colour, with large numbers of small white stones of all sizes.

(40-42). From Nauru, obtained respectively from the coconut belt surrounding the island, from near the lagoons, and from the phosphatic region. The first two contained a very high percentage (70 to 80 per cent.) of calcium carbonate, but in the remaining sample it was only $2\frac{1}{2}$ per cent.

(128-130). Respectively from a native village, from the virgin soil area, and from the central mining area of Ocean Island. This island is subject to drought.

West Indies. Leeward Islands.—(62, 63, and 64). From three widely separated estates (Brighton Estate, Caines Estate, and La Guerite) on St Kitts. The crops grown were not recorded, but all the soils appeared very dry and clayey.

(65 and 66). From the adjacent island, Nevis. They were rather lighter and moister than the St Kitts soils, but the number of protozoa was lower in each case.

(51-55). Antigua, an island which though subject to drought is very fertile. 51, general nursery (Skerret's Estate); 52, garden soil (Cassada); 53, from a ravine (Lee Ghaut, Bendall's Estate); 54, new ground from the same estate; 55, sugar-cane nursery (Skerret's Estate). With the exception of 53, which was sandy, they were all loams of various kinds, 51 being a sandy loam and 52 a much heavier clayey loam.

Windward Islands.—(59-61). From the northern, middle, and southern parts of Santa Lucia, the first and second being from plantations of cacao and sugar respectively, and the third being from a coconut plot

at the Experiment Station. These soils are reported to be very deep and rich, and had the appearance of being good, dark-coloured loams. In 59, however, the numbers of protozoa were decidedly below the average.

(56-58). Grenada, from St John's, St George's, and St Andrew's respectively. Though the Grenada soils are reported to be very fertile, soils 56 and 58 yielded very low numbers of protozoa. 57, however, a black mould from the experiment plot of the botanical garden, yielded rather more than the average number of species.

(146). A rather coarse garden soil from Strathmore in Barbadoes.

Mauritius.—(102 and 103). Woodland and sugar-cane soils respectively from Reduit (alt. 1000 ft.).

(104 and 105). Cultivated soils from Grand Bay (alt. 100 ft.) and Beau Bois (alt. 1000 ft.) respectively.

(106 and 107). Both from Medine (alt. 350 ft.), the former was described as cultivated soil and the latter as a woodland soil.

(108). Cultivated soil from Trianon (alt. 1000 ft.).

(109). Another cultivated soil from Bel Ombre (alt. 300 ft.).

(110). Botanical garden at Curepipe (alt. 1800 ft.).

(111 and 112). Sugar-cane and woodland soils, both from Pamplemousses (alt. 200 ft.).

It is reported that in Mauritius soils in general, though nitrification is slow, general bacterial activity is high, and nitrogen fixers are abundant. The nitrogen content is invariably high compared with

other tropical soils, averaging about 0.3 per cent. The protozoan figures were found to be on the whole also a little above the average.

Tropical and Sub-Tropical; Continental.

Palestine.—(8 and 9). Two very sandy soils from Nes Ziona bearing oranges and almonds respectively.

(10). A clayey soil from Mikve Israel.

(11). From hilly land on the experiment farm at Ben-Shemen, near Ludd; a grey, clayey soil bearing a crop of carubs and olives.

(12). Loam from the experimental grain land in the Merhaviah Israel Valley.

(143). Yellow sand from Jaffa.

North Africa. Egypt.—(88-90). Soils from Giza, the first being market garden soil, the second wheat soil under flood irrigation, and the third pure yellow sand from the desert near the Pyramids. The last contained only 0.006 per cent. of nitrogen, and the loss on ignition was only 1.03 per cent.; yet it yielded a number of protozoa, both flagellates and amœbæ. Even at the spot where this sample was taken, however, traces of dried-up grass occurred, and it is quite reasonable to suppose that wherever the root-hairs of herbage can find soil conditions temporarily favourable to their active functioning, there also are conditions in which protozoa can live.

(91-94). From Bahtim, near Cairo.

(91). A soil bearing a very thin and patchy crop of barley. This was described by Mr Prescott (who sent all the Egyptian samples) as a very alkaline soil,

but, unfortunately, the sample was lost before the *p*H determinations were made.

(92). Garden soil.

(93). Wheat soil under normal rotation.

(94). Unmanured fallow soil following a cotton crop.

Algeria.—(138). A single soil was examined from the experimental farm at Berteaux in the high plateaux region. The soil was strongly alkaline.

Central Africa. Sudan.—(95 and 96). Collected by Sir John Russell in the course of his visit to the Sudan at the end of 1923. Both were heavy black cotton soils from the Gezira research farm at Wad Medani, 95 being irrigated and 96 unirrigated.

Kenia.—(97). Very deep vegetable mould from Kericho in the hill district east of Lake Victoria. The actual rainfall at the spot was not given, but in other parts of the same district it varies from 40 to 100 in.

Congo.—(131 and 132). Virgin forest soil and coffee plantation soil respectively from Lula, near the Stanley Falls on the Congo.

(133 and 135). From the neighbourhood of Sandoa (Katanga) in the southern part of the Belgian Congo; virgin forest and manioc plantation soils respectively.

(134). A clayey soil bearing abundant grasses, from Madimba, near Leopoldville, in Mid-Congo.

The temperature conditions throughout the Congo are very uniform, averaging about 90° F., and the

rainfall is lower than in East Africa, ranging between 16 and 38 in. per annum.

South Africa.—(136). Virgin grass "vlei" soil from the North-East Karroo at Grootfontein in Cape Province. The annual rainfall here averages about 10 to 12 in.

(137). Virgin soil from Cedara, Natal, taken just after heavy rains. The protozoa in soils from both these localities have been extensively investigated by Fantham and collaborators at Johannesburg.[35-38]

Argentine.—These soils, though all taken from the pasture lands in the provinces of Entre Rios and Corrientes, showed an extraordinary range of colour and texture. The annual rainfall in these provinces varies between 39 and 47 in., and whereas Entre Rios is undulating country, Corrientes is flat and in many parts swampy.

(75). A soot-black, sticky, humus soil from Gualeguaychu in Entre Rios.

(76). A dark grey, stiff clay from La Cruz, Corrientes.

(77). A dark brown, sandy soil from San Miguel, Corrientes.

(78). A light-grey loam from Curupicay, Corrientes.

(79 and 80). Sticky, red loams from the higher land of S. Tomé, Corrientes.

(81). From the lower land at the same place as 79 and 80, and rather lighter in colour than 80. Cattle on the pastures from which 78 was taken suffer from osteomalacia said to be due to a deficiency of lime in the soil, but the actual acidity of this

soil was not so great as that of samples 77, 79, 80 and 81.

India.—(144). Black soil from a dry cotton field, near Madras.

(122 and 123). Two samples of wet, paddy soil from the central farm, Coimbatore (Southern India). 122 had been air-dried and was a very fine, light-brown powder. 123, on the other hand, was put into a bottle in its natural condition, with a layer of water standing over it. The inside of the bottle became thickly coated with a ferruginous deposit, probably due to the action of iron bacteria.

(145). Garden soil from Coimbatore, light-brown loam.

(125 and 126). Reddish laterite soils from spice gardens at Kanara, near the western coast of Southern India. Both soils were manured with dung, but, whereas the cardamons grown on 125 were healthy, those from 126, which was a much deeper red in colour, were diseased. The rainfall here is very heavy (about 100 in. per annum) and the temperature warm but very equable. These soils were deficient in lime and in nitrogen.

(119). Unirrigated arable soil from Charoli (Poona); a fine deep black soil. Rainfall about 25 to 30 in. per annum.

(120). Unirrigated and unmanured wheat soil from Gurdaspur in the Punjab; rainfall 34 in.

(121). From the neighbouring district of Jullundur: a fine grey soil which grew wheat and maize and was both irrigated and manured.

(124). A sample of the Indo-Gangetic alluvium from Pusa. It had the appearance of a light greenish-grey clay, and was swampy in the wet season but dry and aerated in the dry season. It grew rice and linseed.

(113 and 114). Powdery grey soils from Cinnamara (near Jorhat, Assam) from the southern banks of the Bramaputra.

The remaining samples, 115 to 118, were rice soils from the Hmawbi Agricultural Station in Burma. They were old alluvial soils and when wet (samples 115, 116) had almost the appearance and consistency of putty. The other two samples had been stored dry.

Influences affecting the Protozoan Fauna of Soils.

Introductory.—For the satisfactory comparison of the faunas of different soil types it is necessary that the soils should have been defined according to some uniform system and examined by uniform methods. In order to satisfy these requirements it is necessary throughout the following sections to limit ourselves to the data obtained from the soils examined by ourselves.

Owing to the fact that the soils had all been stored in tins or bottles for varying periods before they were examined, attempts to estimate the numbers of individual protozoa in them would have been practically worthless as an indication of the degree of protozoal activity in the natural soils. The considerable amount of work that has been done on the protozoa in the various experimental plots of the Rothamsted Farm indicate however that, at any rate within the limits

of the single farm, plots from which a large number of species can be isolated are also richer in individuals than those from which fewer species can be isolated. It seems therefore not unlikely that (contrary to Martin and Lewin's finding [79]) the number of species that can be obtained from any soil is a rough indication of the abundance of protozoal life in it; and it is consequently worth while examining the results obtained from the present investigation to see whether they throw any light on the factors influencing the protozoal population of the soil. It must however be remembered that throughout the discussion it is the numbers of species of protozoa in the soils that are being compared, and that these may probably be taken as indications of the actual numbers of individuals. Recording the protozoa found in the different soils (see Charts 1, 2, 3), only those forms have been included which could be identified; but for our present purpose of comparing the density of population of the soils it is necessary to include all which were recognised as distinct species whether or not they could be identified, and to apply the correction explained on p. 7. This has been done in Table III.

Geographical Influences.—In Table III. the soils have been grouped according to the countries from which they originated. The highest average numbers of species were obtained from Gough Island and Tristan da Cunha, while the lowest were those from South Georgia and Cape Verde Islands. Those from Canada and India were also abnormally low.

When the countries are grouped into larger

TABLE III.

Note.—The figures in clarendon are ones to which the correction explained on p. 7 has been applied.

Country.	Reference No. of Sample.	Total Nitrogen.	H_2O in Air-dried Soil.	*p*H.	Flagellates.	Ciliates.	Amœbæ, etc.*	Testaceous Rhizopods.	Total Protozoa.
Arctic and Antarctic.		Per cent.	Per cent.						
Spitsbergen . . .	43	1·53	8·9	6·3	**1·1**	**1·3**	**0**	**3·5**	**10·9**
	44	0·75	5·1	7·2	**3·2**	**2·7**	**1·1**	**5·1**	**12·1**
	45	0·15	1·1	8·0	**4·3**	**5·3**	**0**	**3·4**	**13·0**
	46	2·85	11·6	6·6	**3·2**	**2·7**	**3·3**	**3·4**	**12·6**
	47	2·47	8·8	6·0	10	5	5	4	24
	48	1·49	51·4	3·9	6	7	6	9	28
	49	0·44	55·9	6·0	5	2	1	5	13
	50	0·38	20·3	5·2	10	3	4	4	21
Average . . .	...	1·26	20·4	6·2	5·4	3·6	2·6	5·3	16·8
Greenland	67	0·06	0·7	3·7	2	1	1	0	4
	68	0·04	0·6	6·0	2	0	1	1	4
	69	1·96	10·5	4·5	3	2	1	0	6
	70	0·79	9·8	7·2	6	3	1	3	13
	71	0·75	7·6	6·4	5	1	1	6	13
	72	0·49	6·3	6·4	3	3	2	9	17
	73A	0·21	5·5	6·2	4	0	0	2	6
	73B	0·42	7·0	5·5	3	0	1	1	5
	74	0·46	4·3	7·2	15	15	10	6	46
Average . . .	...	0·58	5·8	5·9	4·8	2·8	2·0	3·1	12·7
Elephant Island . .	19	0·07	0·3	7·2	5	0	3	0	8

South Georgia . . .	13	2·19	5·6	5·0	3	1	0	3	7
	14	0·15	1·7	5·2	3	0	0	0	3
	15	0·17	1·6	6·2	5	0	0	0	5
	16	0·10	0·7	6·7	2	2	1	10	15
	17	0·21	1·8	4·5	5	0	0	2	7
	18	0·64	4·0	6·2	2	0	1	6	9
Average . . .	...	0·58	2·6	5·6	3·3	0·5	0·3	3·5	7·7
Average for all Arctic and Antarctic soils . .	...	0·78	9·6	6·0	4·6	2·4	1·8	3·8	12·6
Temperate, oceanic.									
Tristan da Cunha . .	20	0·24	2·2	6·5	8	1	4	1	14
	21	0·27	2·5	5·4	17	8	5	3	33
	22	0·46	3·2	6·5	17	6	4	1	28
	23	0·37	3·0	6·6	15	5	4	1	25
	24	0·43	3·0	5·8	17	7	4	7	35
	25	0·39	2·6	6·7	14	8	6	3	31
Average . . .	...	0·36	2·8	6·3	14·7	5·8	4·5	2·7	27·8
Gough Island . . .	26	2·07	5·2	4·4	18	9	3	7	37
	27	2·07	5·8	4·5	10	4	4	9	27
	28	1·77	4·8	4·5	10	9	4	10	33
	29	1·94	5·2	4·5	13	3	3	6	25
	30	2·12	10·1	4·9	11	4	1	7	23
Average . . .	...	1·99	6·2	4·6	12·4	5·8	3·0	7·8	29·0
San Miguel, Azores . .	39	0·11	1·2	7·2	9	4	4	3	20
Average for all Temperate, oceanic soils . . .	...	1·02	4·1	5·6	13·3	5·7	3·8	4·8	27·6

* See p. 7, footnote to Table I.

TABLE III.—*continued.*

Country.	Reference No. of Sample.	Total Nitrogen.	H_2O in Air-dried Soil.	*p*H.	Flagellates.	Ciliates.	Amœbæ, etc.*	Testaceous Rhizopods.	Total Protozoa.
Temperate, Continental.		Per cent.	Per cent.						
England	1	...	...	4·1	8	4	3	0	15
	2	...	...	4·4	8	4	2	2	16
	3	...	...	...	**11·1**	**6·7**	**4·5**	**3·6**	**25·9**
	4	...	...	...	**17·5**	**13·4**	**4·5**	**7·3**	**42·7**
	5	0·005	0·1	7·2	**3·2**	**0**	**3·0**	**0**	**6·2**
	6	...	...	...	**3·2**	**0**	**0**	**10·9**	**14·1**
	7	0·46	2·7	7·5	**4·8**	**0**	**0**	**0**	**4·8**
Average . . .	...	...	...	...	8·0	4·0	2·4	3·4	17·8
Canada	82	0·23	2·6	7·4	7	2	1	1	11
	83	0·38	5·8	7·4	9	1	1	1	12
	84	0·05	0·8	7·2	2	1	0	1	4
	85	0·20	2·5	8·1	7	3	2	3	15
	86	0·14	1·8	7·3	8	0	2	0	10
	87	0·33	3·3	6·2	7	0	1	1	9
	127	0·06	2·1	6·8	1	0	1	0	2
	139	0·11	1·8	8·8	7	2	1	0	10
	140	0·18	1·7	4·5	6	3	1	4	14
	141	0·08	1·9	8·9	6	1	1	1	9
Average . . .	...	0·18	2·4	7·3	6·0	1·3	1·1	1·2	9·6
Japan	98	0·08	2·7	5·4	8	4	3	1	16
	99	0·10	1·2	5·6	10	7	6	3	26
	100	0·18	1·9	5·7	8	1	2	0	11
	101	0·13	3·5	5·8	12	3	2	1	18
Average . . .	...	0·12	2·3	5·6	9·5	3·8	3·3	1·3	17·7

Australia	142	0·13	4·2	8·4	10	8	2	3	23
Serbia	147	0·18	3·9	8·0	7	7	2	2	18
Average for all Temperate Continental soils . .	...	0·16	2·5	6·7	7·4	3·1	2·0	2·0	14·5
Tropical and Sub-Tropical—Islands.									
C. Verde Island—St Vincent.	34	0·02	4·3	7·2	1	0	0	0	1
	35	0·006	6·2	8·5	1	0	1	0	2
	36	0·06	7·8	8·3	4	1	3	0	8
	37	0·21	5·1	8·2	7	6	4	0	17
	38	0·06	0·8	8·2	4	3	4	0	11
Average . . .	...	0·07	4·8	8·1	3·4	2·0	2·4	0	7·8
St Helena	32	0·23	8·1	8·0	9	9	2	0	20
	33	0·37	7·2	5·2	13	6	3	3	25
Average . . .	...	0·30	7·7	6·6	11·0	7·5	2·5	1·5	22·5
St Paul's Rocks . .	31	7·64	8·9	7·1	6	2	3	2	13
Nauru	40	0·20	1·5	7·8	**3·2**	**0**	**1·5**	**0**	**4·7**
	41	0·26	1·8	8·0	**12·7**	**3·3**	**3·0**	**3·6**	**22·6**
	42	0·36	2·6	7·2	**4·8**	**6·7**	**1·5**	**0**	**13·0**
Ocean Island . . .	128	0·23	2·5	7·2	7	4	2	1	14
	129	0·40	3·5	7·4	11	6	1	5	23
	130	0·45	2·8	7·2	6	7	2	2	17
Average . . .	...	0·32	2·5	7·5	7·5	4·5	1·8	1·9	15·7

* See p. 7, footnote to Table I.

TABLE III.—*continued.*

Country.	Reference No. of Sample.	Total Nitrogen.	H_2O in Air-dried Soil.	*p*H.	Flagellates.	Ciliates.	Amœbæ, etc.*	Testaceous Rhizopods.	Total Protozoa.
Tropical and Sub-Tropical—Islands—contd.		Per cent.	Per cent.						
W. Indies—St Kitts . .	62	0·10	1·8	6·9	8·0	3·3	3·0	0	14·3
	63	0·12	1·7	7·2	12·7	6·7	4·5	3·6	27·5
	64	0·08	1·5	7·2	11·1	0	1·5	0	12·6
	65	0·13	4·5	6·8	4·8	3·3	1·5	0	9·6
	66	0·11	4·1	7·2	6·4	3·3	1·5	0	11·2
Antigua	51	0·09	6·1	7·2	4·3	1·3	1·1	0	6·7
	52	0·15	6·3	8·0	4·3	4·0	3·3	1·7	13·3
	53	0·07	3·1	7·2	5·4	1·3	1·1	0	7·8
	54	0·13	4·3	7·2	5·4	4·0	2·2	1·7	13·3
	55	0·11	6·0	7·2	4·8	3·3	1·5	3·6	13·2
Sta. Lucia . . .	59	0·14	8·2	6·3	3·2	1·3	4·4	0	8·9
	60	0·22	2·8	6·5	10·8	5·3	4·4	3·4	23·9
	61	0·12	2·1	6·3	6·5	4·0	2·2	1·7	14·4
Barbadoes . . .	146	0·18	8·0	8·5	12	5	2	2	21
Grenada . . .	56	0·05	8·8	5·6	1·6	0	0	0	1·6
	57	0·16	5·5	7·2	6·4	6·7	7·6	3·6	24·3
	58	0·27	4·5	5·6	3·2	3·3	3·0	0	9·5
Average . . .	...	0·13	4·7	6·9	6·5	3·3	2·6	1·3	13·8
Mauritius	102	0·23	6·2	6·8	5	5	6	1	17
	103	0·37	6·8	7·0	10	4	5	2	21
	104	0·65	7·5	7·0	9	11	7	4	31
	105	0·20	4·6	7·2	11	6	5	2	24
	106	0·27	6·5	7·2	10	5	5	2	22
	107	0·48	7·4	7·2	4	3	5	1	13

	108	0·28	6·8	6·8	4	5	3	1	13
	109	0·24	5·1	7·0	8	4	4	1	17
	110	0·41	7·6	6·6	9	7	3	2	21
	111	0·22	5·9	7·2	6	3	4	2	15
	112	0·24	6·9	7·2	6	2	3	2	13
Average . . .	...	0·33	6·5	7·0	7·5	5·0	4·5	1·7	18·8
Average for all Tropical and Sub-Tropical Island soils	...	0·39	5·1	7·2	6·7	3·9	3·0	1·4	15·0
Tropical and Sub-Tropical—Continental.									
Palestine	8	0·05	1·4	7·2	14·3	6·7	6·0	3·6	30·6
	9	0·01	0·2	8·2	6·4	3·3	1·5	0	11·2
	10	0·10	4·4	8·2	4·8	6·7	1·5	0	13·0
	11	0·05	1·6	8·2	4·3	0	2·2	0	6·5
	12	0·05	6·2	8·2	4·3	2·7	2·2	0	9·2
	143	0·005	0·1	9·1	4	3	1	0	8
Average . . .	...	0·05	2·3	8·2	6·4	3·7	2·4	0·6	13·1
N. Africa—Egypt . .	88	0·14	4·1	7·9	4·8	16·7	4·5	3·6	29·6
	89	0·06	7·5	7·8	8·0	3·3	1·5	0	12·8
	90	0·006	0·1	7·9	4·8	0	4·5	0	9·3
	91	...	...	very alkaline	6·4	3·3	1·5	3·6	14·8
	92	0·15	5·8	8·5	8·0	20·0	4·5	0	32·5
	93	0·13	5·8	8·0	8·0	20·0	6·0	0	34·0
	94	0·10	6·4	8·1	6·4	10·0	7·6	0	24·0
Algeria	138	0·17	5·4	8·7	6	4	1	1	12
Average . . .	...	0·11	5·0	8·1	6·6	9·7	3·9	1·0	21·2

* See p. 7, footnote to Table I.

TABLE III.—*continued.*

Country.	Reference No. of Sample.	Total Nitrogen.	H_2O in Air-dried Soil.	*p*H.	Flagellates.	Ciliates.	Amœbæ, etc.*	Testaceous Rhizopods.	Total Protozoa.
Tropical and Sub-Tropical—Continental—contd.		Per cent.	Per cent.						
Central Africa—Sudan .	95	0·02	6·1	9·15	8	4	5	0	17
	96	0·02	5·7	9·34	6	4	1	0	11
Kenia	97	0·54	7·7	6·8	**9·5**	**6·7**	**4·5**	**0**	**20·7**
Congo	131	0·13	1·1	5·5	7	1	1	5	14
	132	0·08	1·4	6·4	4	6	1	0	11
	133	0·21	1·9	5·6	6	2	1	2	11
	134	0·09	5·4	4·0	2	3	3	0	8
	135	0·08	0·7	4·5	3	1	1	0	5
Average . . .	...	0·15	3·8	6·4	5·7	3·5	2·2	0·9	12·2
South Africa . . .	136	0·26	6·1	8·7	8	5	1	0	14
	137	0·22	6·4	4·7	10	3	1	0	14
Average . . .	...	0·24	6·3	6·7	9·0	4·0	1·0	0	14·0
Argentine	75	0·19	4·4	6·9	10	4	6	0	20
	76	0·10	3·5	6·9	9	1	2	1	13
	77	0·08	0·5	5·1	17	7	4	5	33
	78	0·12	2·3	5·8	6	3	3	0	12
	79	0·14	3·2	5·6	9	3	1	0	13
	80	0·22	4·1	5·0	7	0	4	2	13
	81	0·11	2·8	4·7	8	4	6	4	22
Average . . .	...	0·14	3·0	5·7	9·4	3·1	3·7	1·7	18·0

India—S. India . . .	144	0·03	4·2	>9·0	5	1	1	1	8
	122	0·07	2·6	7·4	11	5	3	1	20
	123	...	...	7·4	10	4	2	0	16
	145	0·06	3·8	9·0	10	8	2	1	21
	125	0·14	1·3	5·4	5	3	3	1	12
	126	0·10	1·4	5·2	6	2	2	0	10
	119	0·037	7·5	8·4	4	1	1	0	6
N. India . . .	120	0·06	1·0	6·8	5	2	1	0	8
	121	0·10	1·2	8·5	6	4	1	2	13
	124	0·10	1·7	8·7	5	3	2	0	10
	113	0·07	0·8	5·2	3	2	1	0	6
	114	0·09	0·8	3·9	7	2	2	0	11
Burma	115	0·08	2·9	6·5	4	0	1	0	5
	116	0·11	3·0	7·0	2	1	1	0	4
	117	0·09	4·1	5·6	4	2	1	0	7
	118	0·09	4·0	5·8	4	1	0	0	5
Average . . .	...	0·08	2·7	6·9	5·7	2·6	1·5	0·4	10·1
Average for all Tropical and Sub-Tropical—Continental Soils .	...	0·11	3·4	7·0	6·7	4·3	2·4	0·8	14·2

* See p. 7, footnote to Table I.

geographical units, the temperate oceanic islands are found to yield much the highest average for all types of protozoa. The numbers obtained from tropical islands and from temperate and tropical continental areas are very similar. The arctic and antarctic samples give markedly low averages except for testaceous rhizopods, which are abundant in these soils and which are scarcest in the tropical soils.

It would however be unwise to lay too great stress on these geographical variations, for, as has already been pointed out, of all the samples the one richest in protozoa was one from Greenland, which seems to indicate that when local conditions are favourable the general climate is unimportant.

It is generally stated that tropical soils are characterised by a deficiency of nitrogen and of organic matter and by a tendency to acidity resulting from leaching with hot rains. But although the soils examined were not specially selected (with the exception of the last 14 samples, 134 to 147, which were chosen as giving extreme cases of high or low hydrogen-ion concentration) and although they represent an extremely wide range of soil types, they do not show these peculiarities to any marked degree. The tropical islands give figures for nitrogen content and loss on ignition almost twice as high as those obtained for soils from temperate continental areas, which were remarkably uniform in this respect, while the corresponding figures from tropical continental areas were not on the average appreciably lower than those from ordinary English farm soils.

The extraordinary richness of the Tristan da Cunha and Gough Islands soils in nitrogen and consequently presumably in organic matter may account for the high numbers of protozoa found in them; but if this were the main determining factor we should have expected the arctic and antarctic soils to be the next richest in protozoa. This, as has already been pointed out, only holds in the case of the testaceous rhizopods.

Influence of Rainfall.—The great abundance of protozoa in soils from temperate oceanic islands suggests that possibly rainfall is one of the principal factors influencing their development. A simple comparison of the effects of rainfall in widely separated areas is however impossible, since a rainfall which is sufficient to produce moist conditions in a temperate climate may represent conditions of drought in the tropics. It is necessary therefore to limit our consideration of this factor to areas where other conditions are fairly uniform. This has been done in two cases (Table IV.). Mauritius is a relatively small but mountainous island, and the samples obtained from it, though coming from very varied altitudes and subject in consequence to very differing amounts of rain, were on the whole very uniform in other respects. Table IV., however, shows clearly that the differences in rainfall do not appreciably affect the numbers of protozoa found. Similarly no connection can be seen between the numbers of protozoa and the rainfall in the case of the West Indian soils. In this connection it is worth recalling that in work on the daily and

seasonal changes on the numbers of protozoa in a Rothamsted field[26] no correlation could be found between these two factors.

TABLE IV.—*Influence of Rainfall.*

Annual Rainfall in Inches.	No. of Cases.	Flagellates.	Ciliates.	Amœbæ.	Testaceous Rhizopods.	Total Protozoa.
West Indies.						
St Kitts: 38, dry	5	8·6	3·3	2·4	0·7	15·0
Antigua: 45·6, subject to drought	5	4·8	2·8	1·8	1·4	10·9
Barbados: 60 . .	1	12·0	5·0	2·0	2·0	21·0
Sta. Lucia: 70 to 120	3	6·8	3·5	3·7	1·7	15·7
Grenada: up to 200 .	3	3·7	3·3	3·5	1·2	11·8
Mauritius.						
30 to 35 . . .	3	7·7	6·3	5·7	2·3	22·0
45 „ 50 . . .	3	6·7	3·0	3·7	1·7	15·0
70 „ 75 . . .	3	6·3	4·7	4·7	1·3	17·0
100 „ 120 . . .	2	10·0	6·5	4·0	2·0	22·5

Soil Protozoa and Vegetation.—Table V. shows the connection between the numbers of protozoa and the type of vegetation growing on the soils. Garden soils are decidedly the richest, especially in species of ciliates. Pasture soils are however richer in testaceous rhizopods. This difference between testaceous rhizopods and the other protozoa is paralleled in the algæ, among which the diatoms are more abundant in arable soils than in grassland, while the blue-green algæ are more numerous in grassland than in arable soils.[99]

It is rather striking to find that even in the 11 soils described as quite barren of vegetation there was an average of 8.3 species of protozoa.

Effect of Irrigation.—Table V. also shows that irrigated soils contain fewer species of protozoa than the average. It may be that in such soils special types of protozoa develop which are unable to survive the conditions of storage. Or it may be that under such conditions the assumption made

TABLE V.—*Influence of Vegetation and Soil Type.*

	No. of Cases.	Flagellates.	Ciliates.	Amœbæ.	Testaceous Rhizopods.	Total Protozoa.
No vegetation . .	11	3·9	1·3	1·9	1·3	8·3
Mosses, etc. . . .	3	3·7	1·6	2·4	1·1	8·9
Woodland . . .	8	6·1	2·4	2·6	2·0	13·1
Plantations . . .	15	6·5	3·1	2·6	1·1	13·2
Virgin soils and pastures	38	7·0	3·1	2·2	3·3	15·5
Arable	38	8·2	4·8	3·0	1·4	17·5
Gardens . . .	11	7·7	8.1	3·9	1·9	21·6
Irrigated soils . .	11	6·4	2·6	1·8	0·3	11·0
Laterites . . .	4	6·8	2·0	2·5	0·8	12·0
Sandy soils . . .	15	6·0	2·3	2·1	1·5	11·9
Clay soils . . .	8	4·6	2·3	2·0	0·1	9·0
Peaty soils . . .	7	4·0	2·4	1·8	4·7	12·9

on p. 24 does not hold good, and that though the number of species found may be low, the number of individuals of these species may be high. Consequently these results must not necessarily be taken as indicating that protozoal activity is decreased by irrigation.

Influence of Soil Type.—In the last part of Table V. a number of soils which can definitely be grouped into distinct types have been selected. In each case the average number of protozoa found is rather low. The most striking differences between

them are shown by the testaceous rhizopods which are almost absent from the clays but relatively very abundant in the peats. The abundance of these shells in peaty soils was recognised long ago by Müller [81] and others.

Protozoa and Bacteria.—In view of the fact that most of the soil protozoa are bacterial feeders it is probable that the relation between the numbers of protozoa and of bacteria is fairly close. In this connection the recent work of Cutler and Crump [25] is of special interest as it demonstrates that not only the final density of the protozoal population in a culture, but also the rate at which it multiplies are dependent upon the numbers of bacteria present. Bacterial counts on soils which have been stored give, of course, little indication of the number of bacteria in the fresh soil, but in the case of sets of samples from neighbouring localities taken at the same time, simultaneous counts do probably give a rough idea of the relative abundance of bacteria. With the 3 samples from Grenada and the first 5 samples from Spitsbergen, simultaneous counts were therefore made on Thornton's medium, and the parallelism in each case between the results and the numbers of species of protozoa in the same soils was very close (Table VI.). The testaceous rhizopods were again an exception, the highest number in the Spitsbergen soils occurring in samples in which the bacterial numbers were lowest. The similarity between the vertical distributions of protozoa and bacteria, referred to below, further supports the idea that the protozoal

population is determined mainly by the quantity of bacteria available for food.

TABLE VI.—*Relationship between Soil Bacteria and Protozoa.*

	Bacteria (millions per gram).	Flagellates	Ciliates	Amœbæ	Testaceous Rhizopods	Total Protozoa.
Spitsbergen—43 .	1·3	1·1	1·8	0	8·5	10·9
44 .	4·87	3·2	2·7	1·1	5·1	12·1
46 .	6·25	3·2	2·7	3·3	3·4	12·6
45 .	12·65	4·3	5·3	0	3·4	13·0
47 .	54·5	10	5	5	4	24
Grenada—58 .	4·35	3·2	3·3	3·0	0	9·5
56 .	4·55	1·6	0	0	0	1·6
57 .	7·85	6·4	6·7	7·6	3·6	24·3

The close connection between the numbers of protozoal species and of bacteria in the soil has already been commented upon by Fellers and Allison.[39]

The Vertical Distribution of Protozoa in the Soil.

England.—Sample 3: this sample was taken at a depth of about 4 in. from among the roots of the grass growing in the thin layer of soil overlying the gravel. Another sample was taken from the side of a gravel pit immediately below at a depth of about 4 ft. The latter yielded a few of the common species of flagellates and the amœba *N. gruberi*, but a similar sample taken a few months later from a new cutting with greater care to avoid surface contamination proved quite free from protozoa. It appears therefore that in gravel subsoil protozoa are entirely absent at this depth, the few found on the first occasion being

no doubt introduced after the pit had been dug by dust blown against it or by surface soil falling over it.

Greenland.—For samples 73A and 73B the former was taken immediately below the humified surface layer and the latter at a depth of 45 cm. No information was supplied as to any special precautions taken in obtaining the latter sample and it yielded nearly as many protozoa as the surface sample.

Sudan.—(95). Nine samples were taken here at regular vertical intervals, the first being at the surface and the last at a depth of 8 ft. At the surface 0.92 million bacteria per gramme and 14 species of protozoa were found. At depths of 1 and 2 ft. the bacteria were too few to be counted with the dilutions used, but 6 species of protozoa were found in each sample. Below 2 ft. the numbers of bacteria were negligible and protozoa entirely absent. A similar result was obtained with the other Sudan soil No. 96. Here 7 samples were taken at depths ranging down to 2.59 metres. At the surface 1.58 million bacteria per gramme were found and 11 species of protozoa. At 0.60 m. no bacteria appeared on the plates but 2 species of protozoa were found. Below this depth no protozoa could be detected.

Kenia.—(97). This was a very deep soil, and samples taken at depths of 4 in. and 4 ft. respectively showed little difference in appearance. In taking the deeper sample special care was taken to prevent any surface soil from falling down and so contaminating the sample. In spite of this 6 species of protozoa

were found in cultures from the deeper sample as compared with 11 from the surface one.

These results are in accord with those found by other investigators and with our knowledge of the distribution of the rest of the soil flora and fauna. They have further been confirmed recently by the work of L. K. Losin-Losinsky, whose unpublished investigations on the protozoa of the steppe soils of Turkestan Mme. Rokitzkaia has kindly allowed me to see. He found that most of the protozoa are confined to the top 20 cm. of soil, but that one holotrichous and one hypotrichous ciliate and a few species of flagellates extended down to twice this depth.

Rothamsted Soils.—Attempts were made in May and June 1923 to carry this inquiry a stage further by making actual counts of the numbers of protozoa and of bacteria at different depths in Rothamsted soils. The protozoa were counted by the dilution method,[26] but unfortunately the distribution of the organisms in the cultures of different dilutions was so erratic that little reliance could be placed on the actual figures obtained. The first set of samples was taken at depths of 0, 6, 12, and 18 in., and the bacterial numbers were 6.25, 4.50, 0.35, and 0.15 millions per gramme respectively. The protozoa appeared to be slightly more numerous at 6 in. than at the surface and were very scarce in the lower depths.

The second series was taken at depths of 1, 3, 5, and 9 in., and gave bacterial counts of 4.55, 12.06, 7.1, and 3.06 millions. In this case the protozoa

apparently reached their maximum numbers at the third depth (5 in.) and showed a considerable falling-off at the lower depth.

The digging of foundations for some new labora-

FIG. 2.—Photograph of excavations for foundations of the new laboratories at Rothamsted, from which depth samples were obtained.

tory buildings in April 1923 provided an opportunity for taking samples at greater depths (Fig. 2). Before taking each sample the face of the pit was flamed with a blow-pipe to prevent contamination and a horizontal bore made with a sterile auger.

The first sample, consisting of clay slightly discoloured with soil, was taken at a depth of 2 ft. It yielded 50,000 bacteria per gramme, but of protozoa only a single species of amœba (*Nægleria gruberi*) could be found and this was present in very small numbers. A similar sample taken about three weeks later gave a small number each of *Cercomonas*, *Heteromita*, and *Nægleria*, and 250,000 bacteria per gramme. At a depth of 4 ft. the clay was quite pure and free from soil and the sample contained 100,000 bacteria per gramme and a small number each of *Cercomonas*, *Heteromita*, and *Nægleria* (about 200 per gramme of each), and a very few each of *Oikomonas*, *Hartmanella*, and *Lecythium* (*Chlamydophrys*). Almost all of these were, however, in the encysted condition.

Clay from a depth of 8 ft. gave a similar result, viz. bacteria, 50,000 per gramme, and a few each of *Cercomonas*, *Heteromita*, *Oikomonas*, *Sainouron*, and *Nægleria*, apparently all encysted.

Near this point a pinnacle of chalk rose up to within about 8 ft. of the surface. A sample of this chalk yielded 50,000 bacteria per gramme and a few *Cercomonas*.

It appears therefore that in a clay subsoil the protozoa are quite negligible and probably all of the few that do occur are encysted. This does not, however, exclude the possibility that in exceptional cases protozoa may occur at considerable depths. Thus Kofoid[66] records that he has obtained *N. gruberi* (whether active or encysted is not stated) from clay and rock talus at a depth of 20 ft.

Influence of Chemical and Physical Properties of the Soils.

In order to obtain a simple classification of the soils according to their chemical and physical characteristics the following determinations were made on each of 141 of the samples (the remaining 7 samples being either too small for analysis or else having been lost): total nitrogen content, loss on ignition, moisture content of air dried soil, and hydrogen-ion concentration (see Table III.). The first three of these determinations were made under the direction of Mr G. C. Sawyer of the chemical department, to whom I am very greatly indebted for having undertaken this laborious work. The pH determinations were mostly made by Mr Cutler and myself using the Spurway method.[118] The scarcity of soils falling in the range of pH 7.5 to 8.0 suggests that for slightly alkaline soils the method as employed was not satisfactory, but there seems no reason to doubt that it was accurate enough for the purposes of the coarser grouping employed throughout this discussion.

As would be expected, a very close connection was found between the nitrogen content and the loss on ignition of the soil, the two series of determinations running parallel except in a few cases. The exceptions were nearly all strongly alkaline soils with low nitrogen content but giving a high loss on ignition, probably owing to loss of carbon dioxide from the contained carbonates. In view of the general similarity of the two determinations the data for the loss on ignition were discarded and the total nitrogen was

taken as the sole criterion of the amount of organic matter in the soil.

The hygroscopic moisture, as measured by the water content of the air-dried soil, may similarly be taken as the basis for a rough classification according to the physical properties of the soil, since it depends on the size of the soil particles and the amount of colloidal matter present.

The actual moisture contents of the soil samples were not determined, but in any case they would have given little satisfactory information about the natural condition of the soils, since the values would have been affected so much by the varying conditions of storage and by the season (*i.e.*, whether during a drought or after good rains) at which the samples were taken.

Naturally many other chemical and physical factors probably influence the protozoal fauna of soil, but they have had to be ignored owing to the great amount of labour that the analyses would have required. In view of Atkins' and Harris' recent discoveries[6] on the effects of dissolved phosphates in limiting the number of freshwater organisms, data for the available phosphates in the soils would have been of great interest. It is, however, for the present necessary to limit ourselves to the consideration of the three more easily obtained factors already mentioned.

Statistical Methods.

A five-fold grouping of the soils into Low, Rather low, Medium, Rather high, and High with respect to each of the factors, nitrogen content, hygroscopic

TABLE VII.

	Group.	Range of Group.	No. of Cases.	Average No. of Species of				Total Protozoa.
				Flagellates.	Ciliates.	Amœbæ.	Testaceous Rhizopods.	
		Per cent.						
Total nitrogen	L. (low) .	0·0 to 0·100	42	5·4	2·2	1·9	0·4	9·9
	R. L. (rather low)	0·101 „ 0·200	41	6·7	4·6	2·7	1·7	15·7
	M. (medium)	0·201 „ 0·300	21	7·6	3·6	2·9	1·4	15·5
	R. H. (rather high)	0·301 „ 0·500	19	9·3	4·7	3·1	2·8	19·9
	H. (high) .	> 0·500	18	7·4	4·3	2·7	5·2	19·6
Water content of air-dried soil	L. . .	0·0 to 2·0	40	6·2	2·3	2·0	1·4	11·9
	R. L. . .	2·01 „ 4·0	31	8·3	3·7	2·4	1·6	16·0
	M. . .	4·01 „ 6·0	32	7·0	5·5	3·0	2·3	17·8
	R. H. . .	6·01 „ 8·0	24	6·6	4·1	3·2	1·5	15·4
	H. . .	> 8·0	14	6·2	3·4	2·4	3·4	15·4
*p*H		*p*H						
	L. . .	3·5 to 4·75	14	7·3	3·6	2·6	3·6	17·1
	R. L. . .	4·76 „ 6·0	27	7·6	2·9	2·3	2·0	14·8
	M. . .	6·01 „ 7·25	59	6·7	3·5	2·9	2·1	15·2
	R. H. . .	7·26 „ 8·5	27	6·6	4·7	2·5	1·0	14·8
	H. . .	8·51 „ 9·75	14	6·6	4·6	1·7	0·6	13·5
Do. Fantham and Taylor's data	Acid . .	> 6·0	20	3·35	2·75	1·85	1·00	8·95
	Feebly acid .	6·0 to 7·0	19	3·52	3·42	2·31	1·11	10·36
	Neutral .	about 7·0	2	4·5	2·5	1·0	1·5	9·5
	Feebly alkaline	7·0 to 7·6	7	2·7	3·1	1·6	0·7	8·1
	Alkaline .	7·6	1	5·0	2·0	8·0	3·0	18·0
Do. Fantham and Paterson's data	...	5·5 to 5·9	1	2·0	1·0	...	...	3·0
		6·0 „ 6·4	19	4·7	3·7	2·2	1·8	12·4
		6·5 „ 6·9	17	4·8	4·1	2·1	2·0	13·0
		7·0 „ 7·4	8	4·0	5·4	2·4	1·6	13·4
		7·5 „ 7·9	10	4·4	4·8	2·4	1·5	13·1
		8·0 „ 8·4	3	3·3	2·3	2·3	1·0	8·9
Do. do. water-logged soils.	...	5·0 „ 5·4	1	3·0	1·0	...	2·0	6·0
		5·5 „ 5·9	0	...	...	...	...	...
		6·0 „ 6·4	2	3·5	3·0	...	2·0	8·5
		6·5 „ 6·9	6	2·8	3·0	0·8	1·2	7·8
		7·0 „ 7·4	6	3·3	1·0	1·7	1·3	7·3
		7·5 „ 7·9	2	2·5	2·0	...	1·0	5·5

moisture, and pH value, was made. The average numbers of species of each class of protozoa in these groups are set out in Table VII. The information obtainable from such averages is however by no means exhaustive, especially as some of the factors involved (*e.g.* nitrogen content and hygroscopic water) are not altogether independent of one another. Some measure of the relative importances of these factors is therefore

TABLE VIII.

Grouping of Soils with respect to Numbers of Species of the Different Classes of Protozoa for Calculation of Correlations.

	Flagellates.		Ciliates.		Amœbæ.		Testaceous Rhizopods.	
	No. of Spp.	No. of Cases.	No. of Spp.	No. of Cases	No. of Spp.	No. of Cases.	No. of Spp.	No. of Cases.
L. (low) .	1 to 3	19	0	22	0	12	0	59
R.L. (rather low)	3·1 „ 6	55	1·0 to 2	33	1·0 to 1·5	49	1·0 to 1·5	23
M. (medium)	6·1 „ 9	34	2·1 „ 4	44	1·6 „ 2·5	20	1·6 „ 2·5	18
R.H. (rather high)	9·1 „ 12	19	4·1 „ 7	28	2·6 „ 4·5	41	2·6 „ 4·5	23
H. (high) .	>12	14	>7	14	>4·5	19	>4·5	18

required, and a further five-fold classification of the soils with respect to the numbers of species of each of the classes of protozoa was accordingly drawn up (Table VIII.) and a series of correlation tables made. The use of correlations is however very limited owing to a variety of considerations. In the first place the number of soils is small for the purpose and the experimental errors probably very large. Also a glance at Table VII. shows that only in a few cases is there more than a very rough approach to a linear

regression. Finally the groups adopted in the five-fold classification are arbitrary instead of being of equal range as is required for truly quantitative calculations of correlation, and the distributions of the soils in the groups do not in most cases fall upon a normal frequency curve. No doubt the frequencies could have been fitted to normal curves by the usual statistical manipulations, but the value of the data did not seem to be great enough to justify the labour that this would have involved. In spite of all these sources of error it appeared that co-efficients of correlation or of partial correlation were capable of giving very rough indications of the relative importance of the various factors under consideration, and for this reason they have been utilised.

Correlation between Different Groups of Protozoa.

Throughout the work and in reading the relevant literature one has been struck by the independence of the testaceous rhizopods from the other groups of protozoa. Thus whereas soils containing a large number of species of flagellates are usually also rich in ciliates and amœbæ, the testaceous rhizopods are often abundant in soils where the other groups are scarce, or entirely absent from soils in which they are numerous. A striking example of this is soil 16, a quite barren grit from the bottom of a "mud river" from South Georgia. The other groups of protozoa together totalled only 5 species but the testaceous rhizopods yielded 10—a figure equalled by only one other soil in the whole of the investigation. The

correlations obtained illustrate this point, for whereas those between the flagellates, ciliates, and amœbæ are all fairly high (*i.e.* more than 0.5), those between the testaceous rhizopods and any of these other groups are considerably lower (Table IX., section 1).

TABLE IX.—*Correlation Coefficients.*

I. Between the different classes of protozoa :—

Flagellates and testaceous rhizopods	·339 ± ·050
Ciliates „ „	·324 ± ·051
Amœbæ „ „	·218 ± ·054
Flagellates and ciliates	·585 ± ·038
„ „ amœbæ	·540 ± ·040
Ciliates and amœbæ	·556 ± ·039

II. Between the different soil factors :—

Total nitrogen and pH	−·275 ± ·052
„ „ hygroscopic moisture	·473 ± ·044
pH and hygroscopic moisture	−·133 ± ·056
Total nitrogen and loss on ignition	·602 ± ·036

III. Between the soil factors and the separate classes of protozoa :—

	Flagellates.	Ciliates.	Amœbæ.	Testaceous Rhizopods.
Nitrogen	·244 ± ·053	·155 ± ·055	·256 ± ·053	·584 ± ·038
Hygroscopic moisture	·001 ± ·057	·217 ± ·054	·179 ± ·055	·161 ± ·055
pH (full range)	−·032 ± ·057	·093 ± ·056	·079 ± ·056	−·252 ± ·053
„ (omitting alkaline soils, *i.e.* all with pH > 7·7)				−·590 ± ·037

Partial Correlations.

IV.—

Nitrogen and pH for constant moisture	−·243 ± ·053
„ „ moisture for constant pH	·122 ± ·056
pH „ „ „ nitrogen	−·0035 ± ·057

V.—

Nitrogen and testaceous rhizopods for constant pH	·595 ± ·036
pH and testaceous rhizopods for constant nitrogen	−·1645 ± ·055
pH and nitrogen for constant testaceous rhizopods	−·0826 ± ·056

Nitrogen and flagellates for constant moisture	·277 ± ·052
Moisture „ „ nitrogen	−·132 ± ·056
„ „ nitrogen for constant flagellates	·488 ± ·043
Nitrogen and ciliates for constant moisture .	·0605 ± ·056
Moisture „ „ nitrogen .	·166 ± ·055
„ „ nitrogen for constant ciliates .	·141 ± ·056
Nitrogen and amœbæ for constant moisture .	·197 ± ·055
Moisture „ „ nitrogen .	·068 ± ·056
„ „ nitrogen for constant amœbæ .	·450 ± ·045
Nitrogen and testaceous rhizopods for constant moisture	·583 ± ·038
Moisture and testaceous rhizopods for constant nitrogen	−·1595 ± ·056
Moisture and nitrogen for constant testaceous rhizopods . , . . .	·468 ± ·044

Correlations between the Nitrogen Content, Hygroscopic Moisture and *p*H Value.

Since the hygroscopic moisture of the soils depends largely on their colloidal properties, which in turn are largely determined by the amount of humus present, there is naturally a positive correlation between the moisture contents of the air-dried soils and their total nitrogen contents. The *p*H value, on the other hand, appears to be entirely independent of these other factors, the small negative correlations being apparently entirely due to the fact that the strongly alkaline soils were all deficient in organic matter (Table IX., sections 2 and 4).

Influence of Soil Nitrogen.

The number of flagellates, ciliates, and amœbæ each shows a small positive correlation with the nitrogen content of the soils (Table IX., section 3), but a glance at Table VII. suggests that this may be due entirely to the scarcity of these forms in soils

deficient in nitrogen, for although an increase in the nitrogen content from "low" to "rather low" is associated with an increase in the average number of species of these forms, a further increase of nitrogen from "medium" to "high" is not accompanied by any appreciable rise in numbers. This is rather unexpected, especially in the case of the ciliates, since these were found to be exceptionally numerous in garden soils (Table V.) which are presumably usually characterised by a rather high nitrogen content. It was noticed, however, that of the soils rich in nitrogen in which the flagellates, ciliates, and amœbæ were below the average, practically all were peaty soils from arctic or antarctic regions. On the other hand the soils in which these species were above the average in spite of a low nitrogen content were all tropical or sub-tropical cultivated soils. The last two facts suggest that peat is definitely unfavourable to these organisms, and that possibly climate may have a secondary effect that was not apparent from Table V., so that when allowance is made for these exceptional cases the average numbers of species corresponding to "high" nitrogen would be somewhat higher than those actually obtained, and those corresponding to "low" nitrogen would be somewhat lower. Consequently, within areas where the range of climatic conditions is not so great as that covered by the present investigations, it is likely that the connection between the nitrogen contents of the soils other than peats and the numbers of species of these organisms may be closer than these figures indicate.

The numbers of testaceous rhizopods, on the other hand, show a very marked positive correlation with soil nitrogen. With low nitrogen the tests are almost invariably scarce or entirely absent, and each increment in the average nitrogen content (with one exception) is accompanied by an increase in the average abundance of these organisms, the highest numbers being found in the group of soils with "high" nitrogen content.

Influence of Soil Hygroscopic Moisture.

With all the groups of protozoa except the flagellates it was found that a deficiency of hygroscopic moisture was on the average accompanied by a reduced number of species, and this effect resulted in a small positive correlation between the numbers found and the moisture (Table IX., section 3). The correlation was highest in the case of the ciliates, while with the flagellates the correlation was as near as could be to zero. In view of the positive correlation that had already been found between the hygroscopic moisture and the nitrogen content it appeared possible that this effect was simply an indirect result of the effect of the nitrogen, and therefore, to test this point, partial correlations between each pair of the data: nitrogen content, hygroscopic moisture and number of species of each group of protozoa in turn, for constancy of the third datum were calculated (Table IX., section 5). With the ciliates, where the correlation with moisture was higher than that with the nitrogen, the partial

correlation with moisture for constant nitrogen content was also positive, amounting to 0.166 (which is just significant), showing that this factor may have an influence independent of the amount of organic matter present. With the amœbæ, on the other hand, the partial correlation was only 0.068, while with the testaceous rhizopods it assumed a negative value of 0.1595, suggesting that with deficiency of nitrogen a high hygroscopic moisture (*i.e.*, a fine or colloidal texture) may be actually detrimental. Similarly with the flagellates the insignificant correlation with hygroscopic moisture of 0.001 becomes converted into a partial correlation of −0.132 when the nitrogen is constant.

The Influence of Hydrogen-Ion Concentration.

Contrary to general expectation, the hydrogen-ion concentration appears to have no appreciable effect on the flagellates, ciliates, and amœbæ. The correlations obtained are completely negligible, but this is inconclusive as one would have expected neutral conditions to be most favourable with a marked falling-off as the soils became more acid or more alkaline. Even this, however, does not occur, and one finds, on the contrary, that the average number of species of these three types of protozoa in the soils with pH high or low are not appreciably different from those in neutral soils (Table VII.).

With the testaceous rhizopods the results are different, for alkaline soils are on the average markedly poor in these organisms, while there is a tendency

for high numbers to occur in the acid soils, an effect which gives rise to a correlation of −0.252. As there is a small negative correlation between pH and nitrogen content, and as rhizopod tests have long been known to be abundant in peaty soils, it seemed possible that this effect is largely due to the high amount of organic matter in peaty (acid) soils, and its deficiency, already mentioned, in alkaline soils. But when the partial correlation between soil nitrogen, pH, and species of testaceous rhizopods for constant nitrogen content was determined it was found still to amount to −0.1645 (Table IX., section 5).

Fantham and his collaborators[35-38] have in recent years published lists of protozoa found in a large number of South African soils, and as they also determined the reactions of their samples it is interesting to compare their results with those now under discussion. In the work recorded in their first two papers the reactions to litmus only are given, and the soils are described as Acid, Feebly acid, Neutral, Feebly alkaline, and Alkaline, these groups probably corresponding to pH values of less than 6.0, 6.0 to 7.0, about 7.0, 7.0 to 7.6, and more than 7.6 respectively. In the later work more accurate pH determinations were made. As will be seen from Table VII., in which their results are analysed, they entirely confirm the fact that the reaction of the soil has no appreciable effect on the protozoal fauna. From their data even the testaceous rhizopods seem to be unaffected.

In this connection it is interesting to recall that Perey[91] found over 13,000 flagellates (nearly all active) and 160 amœbæ (half active) per gramme of soil in one of the Rothamsted experimental grass plots in which the pH was as low as 3.65.

These results are paralleled by some interesting unpublished experiments made by S. M. Nasir in this laboratory on the development of soil protozoa in Conn's medium of varying reactions. The lowest pH value at which development took place was 4.5 for flagellates, 3.5 for ciliates, and 3.9 for amœbæ, while all three groups of protozoa were still active at pH 9.75, which was the highest alkalinity tested.

Similarly, Fine[41] found that within the limits of his experiments protozoa were unaffected by acidity, and Collett[19] has more recently shown in greater detail that the toxic effects of acids depend more on the nature of the anions than on the concentration of the hydrogen ion.

Discussion.

From the foregoing sections it is apparent that none of the climatic or soil conditions considered are capable of explaining adequately the relative abundance of protozoa in different soils. The results illustrate also the danger of making generalisations in such matters on the strength of a small number of casual observations. It appears that on the whole the conditions most favourable for the growth of crops are the ones most favourable to the develop-

ment of flagellates, ciliates, and amœbæ, while the testaceous rhizopods flourish best in peaty soils. But any more precise statement of the conditions influencing the development of protozoa in soil must await careful experimental work with a standardised technique. The absence of such a technique renders many of the statements made about the factors influencing the soil protozoa of very little worth. Thus several writers claim that chalk or lime depresses the numbers of protozoa (*e.g.* Nowikoff,[86] Francé[43]). Hutchinson[60] indeed finds that 0.5 per cent. to 1.0 per cent. of lime has a definite "partial sterilising" effect, whereas others (Piettre and de Souza,[94] Waksman and Starkey[117]) find it is advantageous to protozoa. The last authors found, in fact, that a dressing of lime without manure resulted in greater development of protozoa than was obtained with manure but no lime. Such statements may be true of particular soils (though in many cases the evidence on which they are based is very unconvincing), but they are of little value when we are dealing with soils of different types from different localities. The statements frequently made (*e.g.* Feuilletau de Bruyn,[40] Piettre and de Souza,[94] Francé,[43] Nowikoff,[86] Koch,[65] etc.) that moisture is the principal controlling factor, though very plausible, appear to be equally unfounded.

The work of Cauda and Sangiorgi,[18] showing that the rice soils examined by them mostly contain amœbæ only (*i.e.*, no flagellates nor ciliates), is not confirmed by rice soils examined in the present investigations (samples 100, 115 to 118, 122, 123,

124), and no support was found for Coppa's statement[21] that siliceous soils contain more protozoa than calcareous soils.

It is rather noticeable that the investigators who have devoted most careful attention to the distribution of the soil protozoa avoid detailed generalisations of this kind. Thus Fellers and Allison[39] content themselves with a statement that, in general, fertile soils are richer in protozoa than unfertile ones, and that, broadly speaking, "where there are the greatest numbers of bacteria, there also do we find the greatest numbers of protozoan cells and species." Yakimoff and Zérèn[126] also found that the soils containing most protozoa are those manured with dung, while dry marshes and woodland soils contain fewest. With such statements the present results are in entire agreement, and probably they are as much as our present knowledge allows us to assert with any degree of certainty. But even here there are exceptions, as for instance among the Greenland soils, where a poor heath soil (72) yielded more species than soils supporting a luxuriant vegetation, and in some other cases very fertile soils (*e.g.*, 51 from Antigua) yielded surprisingly few protozoa.

Since the foregoing was written, the work of Noland[85] on the factors influencing the distribution of the freshwater ciliates has appeared, affording valuable confirmation of the supreme importance of food supply. In summarising his results he states: "The wide range of tolerance that most ciliates show toward the physico-chemical factors studied, together

with the evident correlation of several of these factors with the food habits of the species, suggests that the nature and amount of available food has more to do with the distribution of the freshwater ciliates than any other one factor."

Distribution of Individual Species.

In general it is not possible to assign characteristic protozoa to any soil type or to any geographical area, and much more detailed and extensive observation is required before the reasons for the presence or absence of a particular species in any particular soil can be defined. The common types of protozoa seem to be absolutely ubiquitous, and the less frequently occurring species are found in soils from such widely scattered localities and of such different types that their presence or absence in any particular sample seems to depend mainly on chance and on the extent of the examination to which the soil is submitted. Thus, to give only two examples, the flagellate *Actinomonas mirabilis* has been recorded from 11 soils, of which 3 were uncultivated soils from Gough Island in the South Atlantic, 3 others from manured potato patches in Tristan da Cunha, 1 from the barren Elephant Island in the Antarctic, 2 from cattle ranches of the Argentine, and the remaining 2 from the wheat land of New South Wales and from the fertile hillsides of St Helena respectively. Similarly, *Monosiga ovata* was found in the following 5 widely separated regions, Tristan da Cunha (potato patch), Argentine (pasture), Coimbatore (India, swampy paddy soil), Ocean Island

(a phosphatic equatorial island in the Pacific), and Congo (virgin forest). It also occurs in farm soils of New Jersey, U.S.A.[39] Probably with more detailed knowledge of the requirements of individual species it would in many cases be found possible to explain their absence from some soils and their presence in others. An interesting problem of this kind is presented by the two common limax amœbæ, *Nægleria gruberi* and *Hartmanella hyalina*. Both are very widely distributed, having been found in 43 and 77 respectively out of the 148 soils, but only in 13 cases were they found coexisting. Even within the limits of the Rothamsted Farm it has been found that in one field *N. gruberi* will be the dominant soil amœba, *H. hyalina* being almost or entirely absent, while in a neighbouring field the position will be reversed. Recently it was desired to obtain a culture of *N. gruberi*, and several samples of soil were therefore taken from a plot from which daily samples had been taken in 1919 and 1920 and which then yielded large numbers of this species and only occasionally a few individuals of *H. hyalina*. But now not a single specimen of the desired species could be obtained, its place being taken entirely by the other.

The Soil Protozoal Community.

Out of approximately 250 species of protozoa which have been recorded from soils there are a small number which can be found in almost every soil, often in very large numbers, and which may therefore be regarded as the dominant soil forms. These

are the flagellates *Heteromita globosa*, *Oikomonas termo*, *Cercomonas* spp., the ciliates *Colpoda cucullus*, and *C. steinii*, and the limax amœbæ *Nægleria gruberi* and *Hartmanella hyalina* (though, as already pointed out, the last two species do not generally coexist). Forms slightly less generally found include the flagellates *Tetramitus spiralis*, *Allantion tachyploon*, *Phalansterium solitarium* (the last two species are commonly found together), *Sainouron mikroteron*, and *Scytomonas pusilla:* the rhizopods *Lecythium hyalinum* (= *Chlamydophrys stercorea*), and *Nuclearia* sp., and a number of ciliates such as *Gonostomum affine*, *Pleurotricha lanceolata*, *Balantiophorus elongatus*, *Enchelys* sp., and *Oxytricha* sp.

Testaceous rhizopods, though scarce or entirely absent from arable soils, are very characteristic of peaty soils. The forms found are the same as those commonly found among mosses, the commonest being *Difflugia constricta*, *Trinema lineare*, *T. enchelys*, *Centropyxis* spp.

Most of these species, as well as those less frequently observed in the soil, with the exception of the testaceous rhizopods, are commonly found in infusions of herbage or of other organic matter, or in the fæces of herbivorous animals, and it is not improbable that the whole of the protozoan fauna of these media is derived ultimately from the soil. At the end of Table XI., however, a list is given of forms which do not appear to have been recorded from any other habitat except the soil, and which may therefore be regarded as soil dwellers in the strictest sense of the word.

While it is true, on the whole, to say that the commonest soil protozoa are ones which are known to be practically ubiquitous in fresh water, and that the majority are species commonly found in water containing a fairly high amount of organic matter, the list also contains the names of organisms generally regarded as belonging to very widely differing habitats, some being found in putrefying liquids and others leading a planktonic existence in clear waters. Hausman[59] has given lists of protozoa found in six different types of habitat, and the following table summarises his results. The figures indicate the number of species found by him, divided into predominant and scarcer forms, while in brackets are given the numbers of these which are also found in soil.

TABLE X.

	Predominant Forms.	Scarcer Forms.
1. Marsh pools	20 (12)	29 (18)
2. Clear cold water with no plants and no organic matter	5 (2)	8 (7)
3. Clear flowing water with abundant plant life	16 (10)	23 (16)
4. Small clear pools with abundant decaying organic matter	10 (7)	27 (18)
5. Warm pools choked with algæ . .	9 (4)	8 (4)
6. Dead leaves	5 (2)	4 (1)

It is striking that roughly the same proportion of soil forms are found in all these widely differing habitats. In Table XI. an attempt is made to summarise what is at present known as to the occurrence of soil protozoa in other habitats. The

data were obtained simply by consulting the standard text-books, etc., as to the supposed natural habitats of the species in question. Since the ecology of protozoa is a practically unexplored field, the descriptions of the habitats given in the books are almost hopelessly vague and depend entirely on the personal taste of the author, so that it is impossible to compare in detail the statements made by different authorities. Table XI. shows, however, the wide range of conditions that can be tolerated by different soil protozoa, and suggests further that the majority of them are most at home in waters rich in organic matter, and that a high degree of aeration is unnecessary. The rhizopod fauna is very similar to that found on wet mosses.

Although most of the soil protozoa are therefore quite common in other environments, there are a considerable number of forms equally common in these other habitats which appear to be either completely absent or very scarce in the soil. As already suggested above, the almost complete absence of so common a ciliate as *Paramœcium* may plausibly be attributed to its inability to form cysts, but in many cases no such explanation seems possible. Thus among the flagellates which Alexeieff[1] describes as "tout à fait ubiquistes: leurs kystes doivent se trouver dans l'air partout" are *Bodo caudatus* and *B. minimus*, which are practically absent from the soil, and *B. edax* and *B. saltans*, which though sometimes found are far from common. A similar case is given by *Coleps hirtus*, of which Noland[84] says,

"Probably no other ciliate is able to live in a wider variety of habitats, or to subsist on a more varied diet." With none of these forms can their absence or scarcity be attributed to the inadequacy of the methods of examining soils, for they are all forms which develop well in cultures. Many other such gaps in the list could be mentioned—the scarcity of ciliates such as *Stylonychia* and *Colpidium*, of testaceous rhizopods such as *Arcella*, or of the heliozoan *Actinophrys* are a few striking cases. With the last organism mentioned an explanation may be found in the absence of suitable food, for in one of the very few soils in which *Actinophrys* has been found the flagellate *Chlorogonium* also occurred which is known to be a favourite food of the heliozoan, and it therefore seems probable that their occurrence together was not accidental.

The presence in the soil of species not known to occur elsewhere, and the absence from it of some very common forms, suggest that the soil forms are not an accidental collection of the less highly specialised types (though, no doubt, this is the description which would apply to most of them), but that we are dealing with a fairly well-defined group, possessing distinctive physiological requirements. More detailed knowledge than is at present available is required both with respect to their own mode of life and to the composition of the rest of the soil flora and fauna before it is possible to say what are the qualities in any organism which make its existence in the soil possible.

The behaviour of some of these organisms in cultures suggests that they can tolerate, and may even prefer, partially anaerobic conditions, but attempts which were made to obtain anaerobic cultures failed. Small quantities of soils 117, 119, 122, and of soil from a manured plot at Rothamsted were inoculated into tubes of sterile media which were evacuated until the pressure was reduced to about 10 cms. of mercury. Much putrefaction occurred in all the cultures, but none of them gave any growth of protozoa. A similar culture of bullock dung yielded a fair number of *Cercomonas* sp., identical with the soil form, developing quite normally under these conditions. The negative results of these soil cultures are not, however, very convincing in view of the fact that many of the soil protozoa live in sewage under anaerobic conditions. Among the forms which, according to Lacky,[69] are common in the septic tank where conditions are almost completely anaerobic, are : *Nægleria gruberi*, *Hartmanella hyalina*, *Vahlkampfia guttula*, *V. limax*, *Euglypha alveolata*, *Bodo* spp., *Cercobodo* spp., *Clautriavia parva* (Lacky's figures leave no doubt that this was identical with *Helkesimastix fæcicola*, Woodcock), *Mastigamœba* spp., *Mastigella simplex*, *Pleuromonas jaculans*, *Holophrya* sp., *Metopus sigmoides*. Among the less common ones were *Amœba proteus*, *Vahlkampfia albida*, *Trinema lineare*, *Chlamydophrys stercorea*, *Entosiphon sulcatum*, *Euglena* spp., *Heteronema* sp., *Menoidium incurvum*, *Peranema trichophorum*, *Petalomonas mediocanellata*, *Polytoma uvella*, *Colpidium* sp., *Cyclidium*

glaucoma, *Glaucoma scintillans*, *Lionotus fasciola*, *Pleuronema chrysalis*, *Prorodon* sp., *Vorticella* sp.

Noland has also shown[85] that among the ciliates which can live in cultures entirely free from oxygen are the soil species: *Colpidium colpoda*, *Colpoda cucullus*, *C. steinii*, *Glaucoma pyriformis*, *Spathidium spathula*, and that *Chilodon cucullus*, *Dileptus gigas*, *Euplotes charon*, *Glaucoma scintillans*, *Paramœcium caudatum* require only minute traces.

It appears therefore certain that when other conditions are favourable, many of the soil protozoa are capable of living anaerobically.

None of the soil protozoa are known to be parasitic though, as already mentioned, many are coprozoic, and it is possible (though very improbable) that some of these may retain their activity in the gut of the animal through which they pass. Others, like *Proleptomonas fæcicola*, are closely related to parasitic forms. The possibility that some of them may pass through stages in which they are parasitic within insects, earthworms, and other metazoa living in the soil is an interesting one which has not been investigated.

A curious feature of some of the flagellates, so far only found in soil, may possibly be an adaptation to life in this habitat, though its significance is quite obscure. Whereas most flagellates have either one or more forwardly directed flagella, or else one directed forwards and another backwards, in these creatures there is a well-developed trailing flagellum but the forwardly directed flagellum is either absent or reduced

to a mere stump quite functionless for purposes of locomotion. Thus *Helkesimastix fæcicola* (first found by Woodcock and Lapage in the dung of goats and sheep) may be regarded as a Cercomonad in

TABLE XI.

Numbers of Species of Protozoa characteristic of various habitats and also found in the Soil.

	Flagellates.	Ciliates.	Amœbæ.	Other Naked Rhizopods.	Testaceous Rhizopods.
Marine	8	18	2	1	6
Mud	4	12	2	0	8
Bottom of ponds	5	14	3	0	16
Stagnant water	44	57	5	4	18
Flowing water	3	13	1	0	3
Water with much organic matter	48	41	2	3	2
Water with little organic matter	4	5	0	0	0
On aquatic plants	17	29	3	4	18
Infusions	17	32	0	0	0
Putrid water	18	26	4	1	6
Sewage, fresh	11	12	3	0	1
Sewage in septic tank (anaerobic)	11	6	3	0	2
Planktonic	16	1	0	0	6
Coprozoic	12	1	0	0	1
Wet mosses	...	...	6	1	45
Dry mosses	...	...	1	0	11
Only in soil	8	0	8	3	2

which the anterior flagellum is very much reduced, *Sainouron mikroteron* and possibly *Allantion tachyploon* as Heteromitidæ in which the flagellum is absent or much reduced, and *Allas diplophysa* as a colourless Phytomonad in which a similar reduction has taken place. The only similar organisms that have been found elsewhere are *Clautriavia*, Massart, *Phyllomonas*, Klebs (which has also been found in

the soil) and the two flagellates *Piromonas* and *Sphæromonas* found by Liebetanz in the stomachs of ruminants. The mode of progression of these organisms is quite obscure as the long flagellum appears to be completely passive. The possibility of special morphological adaptations to soil life is suggested also by the testaceous rhizopods, among which the spinous forms are almost entirely absent. Thus *Centropyxis aculeata* is found only in the variety *ecornis*, and among the species of *Euglypha* it is the glabrous forms such as *E. tuberculata* and *E. lævis* which occur in the soil rather than those such as *E. ciliata*, which bear spiny appendages.

The species found only in soil are:—

Flagellates: *Allantion tachyploon*, *Allas diplophysa*, *Colponema symmetrica*, *Phalansterium solitarium*, *Sainouron mikroteron*, *Tetramitus spiralis*, *Anisonema minus*, *Parapolytoma satura*, and *Cercobodo vibrans*.

Amœbæ, etc.: *Nægleria gruberi*, *Hartmanella hyalina*, *A. diploidea*, *A. agricola*, *A. horticola*, *A. gobanniensis*, *A. glebae*, *A. nitrophila*, *Gephyramœba delicatula*, *Leptomyxa reticulosa*, *L. flabellata*.

Testaceous Rhizopods: *Geococcus vulgaris*, *Difflugia craterella*.

Summary of Conclusions.

1. Of all the soils examined, none, even the most barren, were entirely free from protozoa. The numbers of species found varied in different samples from 1 to 46.

2. Altogether about 250 species of protozoa have been recorded from soils. Of these many occur only very occasionally and cannot be regarded

as true soil forms. Of the remainder a few appear to occur only in soil, but the majority are highly adaptable and not specialised forms, occurring also in many other habitats, especially in water rather rich in organic matter. Most of the coprozoic species occur also in the soil. Some forms common in these other habitats are, however, absent or very scarce in the soil, and the soil forms may therefore be regarded as composing a fairly well-defined community.

3. All the soil protozoa appear to be world-wide in their distribution, the same species occurring in arctic, temperate, and tropical soils. It has not been found possible to associate characteristic species with any particular geographical areas or soil types.

4. Some of the species found in the soil are known to be capable of living under anaerobic or semi-anaerobic conditions.

5. Very few protozoa occur in the sub-soil. Under arable conditions the maximum numbers are generally reached at a depth of about 10 to 12 cms.

6. The influences affecting the number of species in any soil are rather different for the testaceous rhizopods on the one hand, and for the flagellates, ciliates, and amœbæ on the other. For the latter classes the food supply in the form of bacteria appears to be by far the most important factor, since the conditions most favourable to bacterial development are the ones which give rise to the occurrence of the largest numbers of species of these protozoa. Temperature, moisture, reaction, and soil texture are of little importance, but abundance of organic matter

is beneficial except in the case of peaty soils. The highest numbers are found in arable and garden soils. The testaceous rhizopods show a high positive correlation with organic matter, and a negative correlation with the pH of the soil. They are very numerous in acid peaty soils where bacterial development is poor, and scarce or entirely absent in neutral or alkaline cultivated soils.

A Systematic Account of the Protozoa recorded from the Soil.

It is unfortunate that no complete and authoritative account of the free-living protozoa has been published in recent years. The earlier works of Saville Kent [62] and Bütschli,[15] though still often useful, are now quite out of date. For the identification of flagellates the appropriate volumes of the *Süsswasserflora Deutschlands* [72, 88] are almost complete and of great value, and Senn's account of the flagellates in Engler and Prandtl's *Die Natürlichen Pflanzenfamilien* [109] is also very useful. The testaceous rhizopods are adequately dealt with in the Ray Society's volumes by Cash and Wailes [17] and also by Penard,[90] while Leidy's classical monograph is still valuable.[70] For the naked amœbæ one is almost entirely dependent on scattered literature,* though good descriptions of many of the soil forms can be found in some of the medical publications.[31, 11] For the ciliates, Roux's volume [98] is the best available,

* Schaeffer's new monograph, published since this was in the press, is indispensable for the study of the larger amœbæ, but unfortunately does not deal with the smaller forms which predominate in the soil.

though unfortunately it is far from being a complete survey of the class.

In the following pages all the forms which have been recorded from soils are enumerated, and brief descriptions of each are given. The object in view has not been to make these descriptions complete, but to give as clearly and concisely as possible the main features by which each form can be identified without the constant use of the larger volumes and original papers which in many cases are not available for the soil biologist. The more important of the original papers are however included in the bibliography for use in cases where more detailed information is required. In cases of new species, and where it has been possible to make original observations on any of the forms described, fuller accounts are given in the text. In many cases the cysts are very characteristic, and in fact they are sometimes easier to identify than the active organisms. Consequently descriptions and figures of the cysts of most of the commoner species are also given.

Mastigophora.

The classification adopted for this class is based on that employed in the *Süsswasserflora* by Pascher and Lemmermann.[72, 83]

ORDER 1. — PANTOSTOMATINÆ. NAKED, COLOURLESS FLAGELLATES, CHARACTERISED BY THE FACT THAT THEY CAN INGEST FOOD (USUALLY BY MEANS OF PSEUDOPODIA) AT ALL POINTS ON THEIR SURFACE AND NOT ONLY AT A SINGLE MOUTH REGION. THEY POSSESS ONE OR MORE FLAGELLA AND ARE USUALLY MORE OR LESS AMŒBOID.

They are rather characteristic of decaying matter, mud, etc., and of waters rich in organic matter, only a single species being planktonic. The soil forms appear to be exclusively holozoic. Of the two families comprised in this order one (the Holomastigaceæ) is not represented in the soil fauna. The other (the Rhizomastigaceæ) is represented by the following forms :—

Actinomonas mirabilis, Kent.—One of the most beautiful of the flagellates, consisting of a small spherical body surrounded (like a Heliozoan) by fine radiating processes. Length 10 to 11 μ. It has a fine stalk equal in length to two or three times the diameter of the body, and a single flagellum which enables it to move forwards slowly and jerkily when the end of the stalk is not firmly anchored to some foreign body. This species does not seem to have been recorded by other soil investigators, but it was found in 11 soils examined in this laboratory, coming from Gough Island, Tristan da Cunha, Elephant Island, St Helena, Argentine, and New South Wales.

Cercomonas Duj. (*Dimorpha*, Klebs). — In this genus there are two flagella, one directed forwards, and the other, though arising at the anterior end, directed backwards and generally adhering to the body, which is often drawn out into a sort of "tail" along the distal part of this flagellum. The body is amœboid especially at the hind end, while the front end is often pointed. The two commonest species are *C. crassicauda*, Alexeieff, and *C. longicauda*,

Stein, which are distinguished by the following features [1, 81] :—

	C. longicauda.	*C. crassicauda.*
Size . . .	5 to 10 μ × 5 to 7 μ.	10 to 16 μ × 7 to 10 μ.
Anterior flagellum	3 to 4 times body length.	Subequal: each slightly longer than the body.
Posterior flagellum	Slightly longer than the body.	
Karyosome . .	Relatively small.	Relatively large.
Diam. of cysts .	4 to 6 μ.	5 to 6 μ.
		"Tail" always stouter than in *C. longicauda.*

Characters such as size, length of flagella, etc., are extremely variable, and consequently in a mixed culture it is usually quite impossible to identify the species satisfactorily.

C. crassicauda is the form most commonly found and is one of the most abundant and universally distributed of all the soil protozoa (Plate II., Figs. 2, 3).

The cysts of these two species are very similar and are easily distinguished from those of the other common soil flagellates (Plate I., Figs. 1, 2, 3). They are spherical and have an outer wall which is smooth and generally colourless (in media such as hay infusion it is often stained brown). It is not perforated by any pores. Within this wall are the protoplasmic contents with a central nucleus surrounded by a characteristic hollow sphere of refringent granules.

Forms of *Cercomonas* which cannot be placed in either of these species occur occasionally in soils but have not been identified.

Cercobodo.—This genus differs from *Cercomonas* in having the posterior flagellum free from the body for the greater part of its length.

C. agilis, Moroff.—The free-swimming form is elongated, tapering to a point at the ends, and swims rapidly with a spiral movement (Plate IV., Fig. 4). It has also an amœboid phase in which fine branched pseudopodia are often formed. Length 10 to 14 μ, width 2 to 5 μ. Only occasionally found in soils, viz., in samples from the Azores, Sudan, and Burma.

Cercobodo vibrans, n. sp.—Broader in shape than *C. agilis*, sometimes quite spherical; length about 15 μ; movements vibratory, not spiral; amœboid phase often with fine, sometimes branching, pseudopodia (Plate III., Figs. 1, 2, 3). This organism is apparently quite new though it is widely distributed in the soil, having been found in 41 of the 148 soils examined. A preliminary description was published under the name of sp. δ in a previous paper [100] which can now be supplemented as follows:—

Shape.—Plastic and variable; usually broad and rounded at the anterior end and narrowing to a blunt point behind; sometimes practically spherical, and sometimes the anterior end is drawn out to a short point at the base of the flagella.

Size.—Length about 15 μ; occasionally smaller ones of 10 to 12 μ are found and very small individuals about 6 μ in length have been observed. The largest specimens seen were about 20 μ long.

Nucleus.—Usually visible in the living unstained condition: situated at or just in front of the centre of the body. It is a typical vesicular nucleus with a fair amount of peripheral chromatin.

Flagella.—In the free-swimming form the flagella arise close together at the anterior end, one being directed straight forwards and the other straight backwards or slightly to one side. The former is a little longer than the body, and the latter usually twice the body-length. Usually the hind flagellum is quite free except at the point of insertion (unlike that of *Cercomonas*), but sometimes it

passes for a short distance through the body and thus appears to be inserted laterally. When the organism passes into the amœboid condition the two flagella usually seem to arise from opposite sides of the body (when the earlier description and figures were published it was supposed that only one flagellum was retained in this phase but this was a fault in observation due to the fact that one of the flagella is often concealed by the body of the organism. In stained preparations the two flagella are always found to be present). The flagella arise from two separate basal granules, which in the free-swimming condition are situated close together at the surface of the nucleus, but in the amœboid forms they often move apart (usually, but not always, remaining still in contact with the nucleus) and are then joined together by a connecting strand.

Pseudopodia.—In the flagellate condition short, finger-like pseudopodia are not infrequently found on all parts of the body but most often at the posterior end. The amœboid phase sometimes has a single broad pseudopodium, but at other times is surrounded by long, finger-like processes, often branched.

Contractile Vacuole.—Single, usually situated just behind the middle of the body.

Movements.—The mode of swimming of the flagellate form is very characteristic, and is usually the most easily recognised feature of the organism in a mixed culture. The flagella are straight and almost rigid, moving with a rapid vibratory motion which throws the whole body into vibration as if set on strong springs. The progression is jerky but fairly rapid, and takes place along the line of the two flagella, the body of the organism being turned at a small angle to this line.

Nutrition.—This has not been observed. Probably small bacteria are taken up by the pseudopodia, but it is exceptional to find any traces of ingested bacteria in stained preparations, so possibly the nutrition is partly saprophytic. On a few occasions a slight depression resembling a cytopharynx has been observed at the base of the flagella. If this should prove to be a true cytopharynx the inclusion of this species in the Pantostomatinæ would need to be abandoned.

Cysts.—The cysts are not often seen in cultures but are very characteristic. They vary considerably in shape, but are generally roughly ellipsoidal and about $15\,\mu \times 12\,\mu$ in size. The outer wall is thick and apparently mucilaginous, but in some (? older) cysts it is thinner though never refringent, and is then separated by a wide

space from the inner wall. The latter is firm and refringent, appearing as a black line in optical section, and is filled with rather lumpy protoplasmic contents in which the nucleus is not visible. There are generally three or four thinner areas in the inner wall from which faint strands pass outwards, giving an appearance as if the inner cyst were suspended by ligaments within the outer wall. The inner cyst averages about 10 μ in diameter (Plate I., Figs. 4, 5).

Reproduction.—No indications of reproduction have been observed inside the cysts. Occasionally abnormal free-swimming individuals have been seen in which both the flagella are double. These are probably dividing forms, but it has been impossible to observe the whole process of division. As the organism multiplies slowly in cultures and is never present in very great numbers it is obviously a very unfavourable subject for observations on reproduction.

Systematic Position.—Owing to the confusion that at present exists as to the nomenclature and identity of the forms to which this species appears to be most nearly related, it is with great reluctance that I introduce a new specific name for it, as the inadequacy of the definitions of some of the older species makes it possible that the organism is not really a new one. It differs from *Cercomonas* in the freedom of the posterior flagellum and in the greater distinctness of the amœboid and swimming stages. In some respects it agrees closely with *Cercobodo laciniægerens*, Krassilstchik,[67] but the agreement breaks down in several of the minor points. Thus in *C. laciniægerens* the flagella always arise from a short snout ("Schnabel"), which is only sometimes the case in the present form; in *C. laciniægerens* nutrition can be observed at any time, which is certainly not the case here; in *C. laciniægerens* the posterior flagellum is said to be much less easy to observe than the other one, which again is not the case in the present species; and finally, the very striking and characteristic mode of swimming just described is not mentioned in Krassilstchik's description, while the diagrams drawn from life, accompanying his longer paper, show the flagella in sinuous curves which are not characteristic of the free-swimming form of the new species. It is also in many respects similar to *Dimorpha ovata*, Klebs,[63] differing again in the movements and in the fact that in Klebs' figures the contractile vacuole is shown in an anterior position. Neither Klebs nor Krassilstchik give any cytological details from which the mode of insertion of the flagella (probably the most satisfactory basis of classification of these forms) can be ascertained. Blochmann's definition of *Dimastigamœba* is

even vaguer, and owing to the uncertainty as to what organism it actually refers to it is probably safest to discard this name altogether.

Probably the plan least likely to lead to confusion in the present state of our knowledge is to group all these forms under the generic name of *Cercobodo*, Krass., leaving the name *Cercomonas* for the better-known species *C. crassicauda* and *C. longicauda*, in which the trailing flagellum adheres to the body, though Lemmermann and Senn both regard these forms as all belonging to a single genus *Cercobodo*, Krass.

Helkesimastix fæcicola, Woodcock and Lapage.[122]—A small organism, usually only about 6 to 7 μ long, and resembling a *Cercomonas* in which the anterior flagellum is reduced to a very minute stump which can in fact rarely be distinguished at all. The trailing flagellum is thick and easily visible and appears to take no part in the movements of the organism, which consist of a rapid gliding along the surface of the slide (Plate III., Figs. 4, 5). First found in the fæces of farm animals in which Woodcock states that it is very common; it is also quite common in soils, having been found in 25 of the 148 soils examined in the recent survey.

Mastigamœba and Mastigella.—These genera are composed of organisms closely resembling amœbæ but possessing a single forwardly-directed flagellum. They differ from one another in that in the former the flagellum is connected with the nucleus, while in the latter this is not so. As, however, the numbers found in soil cultures are never very great it is generally impossible to ascertain this point, and consequently exact identification is not possible. Organisms belonging to one or other of these genera are fairly

frequently found, and in one case could be definitely identified as *Mastigamœba limax*, Moroff, length 15 to 20 μ (Plate II., Fig. 1). Mastigamœbæ have also been recorded in soils by several other workers, viz., Fellers and Allison, Fantham and Taylor, Fantham and Paterson, Nowikoff, and Yakimoff and Zérèn.

Two other forms which have been recorded from soils should perhaps be mentioned here though their exact systematic position is very uncertain. They are *Protomonas* sp. ? *P. amyli* (Cienk.) and *Ciliophrys infusionum*, Cienk. They differ from the other *Pantostomatinæ* in that the flagella are entirely lost in the amœboid condition, *Protomonas* becoming like a true amœba and *Ciliophrys* almost like a heliozoan. The former was found by Wolff in field soils, and the latter by Fellers and Allison.

ORDER 2.—PROTOMASTIGINÆ. SMALL FLAGELLATES, USUALLY MORE OR LESS AMŒBOID BUT HAVING A VERY FINE PERIPLAST: PSEUDOPODIA WHEN PRESENT NEVER ACT AS ORGANS OF LOCOMOTION: FOOD TAKEN IN ONLY AT ONE POINT: NO CHROMATOPHORES.

The great majority are exclusively holozoic, but some are probably wholly or in part saprophytic.

Family (i.) *Craspedomonadaceæ. — Solitary or colonial flagellates with a single flagellum surrounded at its base by a large collar: in swimming the flagellum is generally directed backwards, acting as a pulsellum.*

Codosiga botrytis, Ehrbg.—A stalked form, one or several cells being attached to an unbranched stalk which is from two to ten times the length of the individual cell; length 8 to 30 μ.

Goodey [49] records this from pasture soil once only.

Monosiga ovata, S. Kent.—A solitary form length 10 to 15 μ distinguished from *Codosiga* by having either a very short stalk or more usually none at all (Plate II., Fig. 10).

Congo, Argentine, India, Tristan da Cunha, and Ocean Island. Fellers and Allison (rare).

Salpingœca.—Somewhat like *Monosiga*, but each cell is enclosed in a transparent sheath or lorica.

Wolff found *S. convallaria*, Stein, and another species, probably *S. ampullacea*, Al. Braun, each of which he describes as being a "Leitform" in field soils, but no other observers have recorded either of them.

Family (ii.) *Phalansteriaceæ*.—*Somewhat like Craspedomonadaceæ, possessing a single flagellum surrounded at the base by a collar which is, however, small (not more than one fourth as long as the cell) and narrow instead of widely spread out: flagellum directed forwards acting as a tractellum. When swimming freely the cells are naked but in the sessile condition they become surrounded by a thick gelatinous sheath.*

Phalansterium solitarium, Sandon [100].—Characters as of the family (Plate III., Figs. 6, 7, 8).

The specific name was given owing to the absence in this species of the well-defined colonies described for the other species of this genus. In cultures, however, considerable numbers are often found, each enclosed in a gelatinous sheath which stick together in large irregular masses (length 10 to 15 μ). As mentioned in the original description, two or more individuals are sometimes found in a single sheath, presumably the products of division in the sheath, but occasionally free-swimming specimens are found with two collars and two flagella arising from opposite poles or with four of each arranged symmetrically, indicating that division also occurs while the cells are

actively swimming. Such individuals have been observed for a considerable time without any further changes taking place, so presumably the process of division is a slow one. This species is easily distinguished from the true "collared flagellates" by the very much smaller size of the collar, and by the nature of the movements which are very characteristic, being produced by a lashing of the flagellum which is so rapid as to make this organ invisible and which imparts to the body a lateral vibration as if it were set on a pivot near its hinder end. In the free-swimming condition this results in a fairly quick forward progression. In the sessile phase the flagellum works in the same way, causing a stream of water with bacteria, etc., to be whirled down towards its base. No ingestion of solid particles has, however, been observed, and stained preparations have not revealed any food bodies inside the cell, so Lemmermann's statement [72] that the other species of this genus are saprophytic probably holds true also of this species.

This species is very widely distributed, having been found in 56 of the 148 soils examined.

Family (iii.) *Bodonaceæ.—Naked, free-swimming forms with two flagella of which one is directed forwards and the other trailed behind* (*except in Dinomonas*)*: in a few cases the anterior flagellum is absent.*

Bodo, Ehrbg. (Prowazekia, Hartmann and Chagas). —More or less elongated forms with the anterior end often forming a short, blunt beak; in addition to the nucleus there is a large deeply staining body (the so-called "kinetonucleus" or "blepharoplast") at the anterior end of the body near the insertion of the flagella. Movement very vigorous and progression generally too rapid to be easily followed.

B. caudatus, Duj.—Very polymorphic, generally flattened and leaf-like and more or less drawn out to a tail behind; length about 10 to 18 μ. Though this is one of the commonest of all the flagellates found in infusions, etc., it is very scarce in soils. Wolff,

however, calls it a "Leitform" in field soils; Martin and Lewin[78] record a flagellate which they "are inclined to identify with *Bodo caudatus* of Dujardin," and I have on two occasions found organisms in soils from Greenland and from Argentine which probably belong to this species.

B. celer, Klebs.—An uncompressed form, rounded behind, tapering and usually curved in front; contractile vacuole anterior; length about 8 to 10 μ.

This is one of the forms which Puschkarew[96] obtained from the air, of which Martin and Lewin[78] said that "all can be found in soil." So far the latter statement has not been confirmed for this species, though flagellates possibly belonging to it were found in soils from Tristan da Cunha and Gough Island.

B. edax, Klebs.—A form very like the previous species but rather larger; length 11 to 15 μ; the flagella arise in a sharp depression just behind the "beak" and the opposite surface of the body is more convex than in *B. celer*. It swims very precipitately in a straight line without any spiral motion (Plate II., Fig. 9).

This species has been found in only 3 of the soils examined here, but occurs occasionally in Rothamsted soils and has also been recorded by Nowikoff and by Kühn, while Yakimoff and Zérèn found it in 7 of the 15 soils they examined.

B. ninæ-kohlyakimov, Yakimoff.—From the very brief descriptions of this species given by Yakimoff[123] it appears to resemble *Heteromita globosa*, Stein, very closely in all except in possessing a "blepharoplast." Seeing that *H. globosa*, which is one of the two or three most abundant and ubiquitous of all soil flagellates,

is not mentioned at all by Yakimoff and Zérèn, while this species, which has not been recorded by anyone else, was found by them in 14 out of 15 soils one feels bound to assume until a more complete account of *B. ninæ-kohlyakimov* is published that their organism was really *H. globosa*, and that the supposed presence of a "blepharoplast" was a faulty observation.

B. saltans, Ehrbg.—Like *B. caudatus* this is a species very abundant in infusions, etc., but not at all common in soil; length 5 to 8 μ. In shape it is somewhat like a shortened *B. edax*, approaching rather more to the shape of a bean. It swims with a smooth, rapid, spiral movement, looking then very like a rather short *Spiromonas*, but it often becomes attached to some solid object by means of the long, trailing flagellum, and then makes from time to time the characteristic very quick and sudden jumps from which it gets its name (Plate II., Figs. 7, 8).

It was found in a Mauritius soil and has also been recorded by Wolff, Goodey, Nowikoff, and Fellers and Allison.

Bodo (*Prowazekia*) *terricolus* (Martin).—A more or less spindle-shaped organism, appearing rather broad and with rounded ends in the figures drawn from stained preparations, measuring roughly 12 μ × 6 μ and having a small contractile vacuole near the base of the flagella. It is "rather an active form, moving with a curious wriggling motion with both flagella directed forwards."

Martin[76] found this organism in a "sick" soil and described the modes of division of the two nuclei and also figured a spherical cyst. It has also been recorded by Cunningham and Löhnis, and by

Thornton and Smith, but I have been unable to find any organism that can be identified with it.

B. parvus has been recorded by Puschkarew and also by Fantham and Taylor and Fantham and Paterson, but the organism referred to by the latter authors is probably that described below as *Heteromita globosa* or *Heteromita lens*.

Fantham and Taylor also record a *Bodo gracilis*, but give no reference by which it is possible to ascertain to what species they refer.

Colponema symmetrica, n. sp.—A flattened elliptical organism approximately equally rounded at the two ends, and having a very marked longitudinal groove on the lower surface which (unlike the groove in *C. loxodes*, Stein) is median and divides the flagellate into two equal halves. Shape quite persistent; never amœboid. Length from 9 to 15 μ. Two flagella arise close together in the anterior part of the groove, the one directed forwards being about one and a half times to twice the body length, and the other, which runs backwards in the groove, three to four times the body length. The nucleus is not visible in the living animal, but is situated at or just behind the middle near the dorsal surface. It is of the vesicular type without any peripheral chromatin and apparently without a nuclear membrane. The organism has never been seen to swim freely; when observed it has always been adhering to the slide by the tip of the long posterior flagellum and jerking constantly backwards and forwards (Plate III., Figs. 12, 13).

It has been found in Hertfordshire soils and from Mauritius, Tristan da Cunha, and St Kitts (West Indies).

Dinomonas vorax, S. Kent.—Egg-shaped, but

with the anterior end rather pointed and somewhat bent over to the ventral surface. Length about 15 to 16 μ. The two flagella are inserted at the anterior end and are both directed forwards.

It is one of the forms found by Puschkarew in the air which Martin and Lewin claimed to have found in soil, but no other observers have confirmed this.

Heteromita, Duj.—Very similar to *Bodo* but without the blepharoplast-like structure. In living cultures it can generally be readily distinguished from *Bodo* by its much feebler movements which are slow enough to be easily followed.

Considerable difference of opinion exists as to the correct nomenclature for these two genera. Hartmann [56] uses the name *Bodo* for those forms *without* a "blepharoplast" and introduces the name *Prowazekia* for the others, but Alexeieff [3] has shown that *Bodo* should be reserved for forms possessing the "blepharoplast," of which the type species is *B. saltans*, and he adopts the name *Prowazekella* for those in which it is absent. The type species of the last genus is however *P. lacertæ* (Grassi) Alexeieff [71] from the intestines of lizards, which differs from the soil species so much in its cytology, in having conjugation of micro- and macro-gametes, and in the multiple fission of the zygote, that it must be regarded as a distinct genus. Alexeieff rejects the name *Heteromita*, Duj., on the grounds that Dujardin applied the name to species of the genus *Bodo*, but of the three species recognised in the *Histoire naturelle des Infusoires*, one (*H. granula*) is so inadequately described as to be quite unrecognisable, another (*H. angusta* = *Spiromonas angusta*) certainly has no "blepharoplast," while the description of the remaining species, though inadequate, is much more reminiscent of the forms at present under consideration than of any of the true *Bodos*. The name *Heteromita*, Duj., is therefore retained for the free-living species without "blepharoplasts," leaving the name *Prowazekella* for the parasitic forms akin to *P. lacertæ*.

H. compressa, Lemm.—An oval form, strongly compressed laterally, with a single anterior contractile

vacuole. Size about 10 to 12μ × 6 to 7μ. Only once found in a soil from Tristan da Cunha.

H. globosa, Stein.—The form recorded under this name is perhaps the commonest of all the soil protozoa. It is ovoid in shape, usually rather broader in front than behind, and the ends are usually rounded though the posterior end is at times amœboid and may be drawn out to a tail. Length from 8 to 12μ. The flagella are inserted close together at the anterior end, the anterior one being about equal to the body length and the posterior one about half as long again. The nucleus (which is visible in the living animal) is anterior, and the contractile vacuole lies just behind it at the centre of the body. The movements (as is general throughout this genus) are much less rapid than those of the *Bodos*. Generally the posterior flagellum trails passively along the microscope slide, the body being turned at a fairly sharp angle to it and moving forwards with a vibratory movement. The cyst is spherical with a large spherical refringent body lying a little to one side of the centre of the protoplasm, which is usually filled with a large vacuole. The cyst wall is usually imperforate with the contents rounded and lying quite freely within it, but in some cultures the cyst contents are connected to the outer wall at five or six points at which the wall appears to be perforated (Plate I., Figs. 6, 7). Whether this difference in the cysts is a specific difference (it seems to persist in sub-cultures) or merely due to differing cultural conditions can only be decided by more careful cultural work.

Frequently, however, instead of forming true cysts, the flagellates simply lose the flagella, and become rounded without forming a wall or a refractile granule. In this condition they can persist for a long time and become motile again when put into fresh medium, but they cannot survive drying, and the resistance to heat is considerably less than that of the cysts. These resting forms are not mere stages in the formation of true cysts, as however long they are kept they do not develop a cyst wall. They occur in varying proportions in all cultures, sometimes in fact almost to the exclusion of cysts, but seem on the whole to be more abundant in synthetic media than in media such as hay infusion.

Here no attempt has been made to distinguish between this form and a smaller one, which is probably *H. lens*, Müller. This differs from the other mainly in size, being usually from 4 to 6 μ in length though smaller forms are sometimes found. Its shape is lenticular and less variable than that of *H. globosa*, and the flagella are relatively longer. It has a thin-walled resting form and cysts like rather small imperforate *H. globosa* cysts. In mixed cultures it is quite impossible to distinguish between large individuals of *H. lens* and small individuals of *H. globosa*, but an attempt was made in cultures containing only one of the forms to determine by actual measurements whether the difference in size was constant. For this purpose the active flagellates were of little use owing to the inconstancy of their shapes. The cysts too were rather unsatisfactory owing to the fact that sometimes the cyst wall is farther away from the cyst contents than at other times (presumably an osmotic effect): in fact, in the most swollen cysts of all a second cyst wall is often present between the outer wall and the protoplasmic contents. The resting forms however gave very constant results, the mean diameters lying between 4.2 μ and 5.0 μ for *H. globosa* and between 3.3 μ and 4.0 μ for *H. lens* whatever the locality from which the cultures were obtained or the media in which they were growing. It appears therefore that the two forms are actually quite distinct, but it was impossible to carry the investigation further owing to the difficulties involved in obtaining single organism cultures which are necessary for critical experimental work.

Both forms are practically ubiquitous in soils, and probably some of the species recorded by other observers are identical with these, *e.g.*, *Prowazekia ninæ-kohlyakimov*,[126] *Bodo ovatus*,[116, 120] *Bodo parvus*.[35, 36]

H. obovata (Lemm.).—Egg-shaped, narrower in front than behind, not curved, 12 to 16 μ long by 6 to 8 μ wide; flagella inserted at anterior end, anterior flagellum 2/5 body length, trailing flagellum twice body length; contractile vacuole single and anterior.

A flagellate agreeing closely with this description was observed in cultures from soils from St Helena, Gough Island, and Tristan da Cunha.

H. ovata, Duj.—A large (21 $\mu \times$ 10 μ) ovoid species, distinctly flattened and characterised by the possession of three contractile vacuoles in the anterior part of the body. The movements are slow and jerky.

This is another species concerning which there is considerable confusion. Probably the descriptions by Moroff[80] and Dangeard[28] refer to different organisms, while, as already mentioned, the records by Wolff and Waksman of this species as one of the commonest soil flagellates almost undoubtedly refer to *H. globosa*. Flagellates which seem identical with Stein's *H. ovata* were found in soils from Tristan da Cunha, Burma, and Canada, and it has also been recorded from South Africa by Fantham and Peterson. Fellers and Allison describe *Bodo* (*Heteromita*) *ovatus* (*caudatus*) S. K. as common in New Jersey soils and give a figure of *Bodo ovatus*, Duj., which is mentioned as being abundant, but the identity of these organisms is doubtful.

H. repens, Klebs.—A form somewhat resembling *H. globosa* but having the anterior end truncated, and with the flagella arising in a lateral groove, has been recorded by Puschkarew (length 9 to 15 μ).

In addition to the species mentioned here a large number of flagellate forms have been observed in soil cultures which probably belong to one or other of the genera *Bodo* or *Heteromita*, but which it has been impossible to identify further, and there is little

doubt that the number of species known to occur in the soil will ultimately be considerably increased.

Phyllomitus, Stein.—Somewhat like a *Heteromita* having no blepharoplast but with a cytopharyngeal groove at the anterior end near the base of the flagella. Two species are known, both occurring commonly in waters rich in organic matter, and both are occasionally found in soils.

In *P. undulans*, Stein (length 8 to 12 μ), the flagella are united for a short distance at their base, and the trailing flagellum is distinctly longer than the anterior one, while in *P. amylophagus*, Klebs, they are equal and not united (Plate IV., Fig. 11). The former species has been found in soils from St Kitts and Santa Lucia in the West Indies, and from Japan and Kanara (South India). Wolff records it as a "Leitform" in field soils and Waksman mentions it as one of the less common soil types. *P. amylophagus* was found in samples from Egypt, Nauru, and St Helena, and Fellers and Allison found a species, which they tentatively identify with it, occasionally present in their soils.

Pleuromonas jaculans, Perty. — Bean-shaped to spherical, 6 to 10 μ in length, amœboid at times; flagella both about two to three times as long as the body, the one directed forwards arising at the anterior end and the one directed backwards inserted about the middle of the body in the ventral concavity.

This species was not found in any of the soils examined here, but Fellers and Allison found it occasionally in their soils. Fantham and his collab-

orators found it widely distributed in South African soils, Wolff calls it a "Leitform" in field soils, and Waksman[116] speaks of *Pleuromonas* sp. as one of the commonest soil flagellates.

Spiromonas angusta (Duj.).—Body narrow, often pointed in front, and, except in the smallest specimens, spirally twisted; length 8 to 12 μ, though much smaller individuals are sometimes found. The flagella arise just behind the anterior end, the one directed forwards being about $\frac{1}{2}$ to $\frac{3}{4}$ the body length, and the other, which is directed backwards, about $1\frac{1}{2}$ times the body length (when the flagellate is killed with a fixative the two flagella are extended rigidly sideways and the longer one is then generally in front of the shorter one). It swims with a rapid spiral movement, and is often easily confused with slender specimens of *Tetramitus spiralis*; but in a strong culture very characteristic sausage-shaped forms can always be found, rounded at both ends and containing at the posterior end a large hyaline mass visible in life which stains very deeply with hæmatoxylin.

Found in 17 of the 148 soils examined here. According to Waksman it is one of the commonest of soil flagellates. Allison found it in 75 per cent. of the American soils he examined, and Wolff found it commonly in German soils. It has also been recorded by Cunningham and Löhnis.

Sainouron mikroteron, Sandon. — Small, rather crescentic flagellates, rounded in front and generally narrower behind; shape constant but occasionally an amœboid condition is assumed; length generally

3 to 5 μ (large forms 10 to 14 μ in length were found in cultures from two soils from Tristan da Cunha and Gough Island, but this is very unusual); flagellum single, arising just below the anterior end and directed backwards (not adhering to the body as in *Helkesimastix*); contractile vacuole absent; movements very like those of a *Heteromita*, fairly rapid and vibratory with the flagellum trailing along the glass slide, or less frequently swimming freely with a somewhat sinuous (not spiral) motion (Plate III., Figs. 9, 10, 11).

Since the original description of this species was published[100] cyst-formation and conjugation have been observed. The so-called "thin-walled" cysts previously described were actually only resting forms similar to those of *Heteromita* described above (p. 85). None of the cultures of the strain from which the earlier observations were made formed true cysts, but cultures of an otherwise perfectly similar strain isolated later encysted freely. The cysts were spherical, 6 to 8 μ in diameter, with a slightly crinkled wall which appeared as a black line in optical section, without any aperture. The protoplasmic contents formed a rounded mass lying freely within the wall, somewhat vacuolated and without any refringent granules. The nucleus was not visible in the unstained cyst (Plate I., Fig. 8). The same culture in which these cysts were found also contained large biflagellate active individuals which when stained showed two complete nuclei lying side by side at the anterior end (Plate II., Figs. 10, 11). There seems little doubt that these were zygotes. The full process of conjugation could not be followed, but the occurrence of these forms in cultures which contained cysts and their absence from those which failed to encyst suggests that cyst formation in this species occurs only after conjugation.

Common in Rothamsted soils and found in 45 of the other soils examined.

Perey found it in 4 out of 5 French soils and Allison in 65 per cent. of the American soils examined.

A larger form, 10 to 12μ long in fresh cultures, and having the anterior end prolonged to a tapering beak at the base of which the flagellum was inserted, was found in cultures of 2 samples of mosses from Spitsbergen [100]. It was probably derived from the soil adhering to the plants, but so far has not been found in pure soil cultures. The name *S. oxu*, Sandon, was given to it.

This genus is very similar to *Piromonas*, Liebetanz,[73] from the rumen of ruminants and may be identical with it, but the descriptions of the latter form are not complete enough for the identity to be certain, and so far I have had no opportunity of examining material of the kind from which *Piromonas* was obtained with a view to making a comparison between the two.

Allantion tachyploon, Sandon.—Shape ovoid or ellipsoidal, rounded at the ends, sometimes slightly crescentic; not at all flexible or amœboid; length 8 to 14μ; flagellum relatively thick, about $1\frac{1}{2}$ times the body length, arising just behind the anterior end and directed backwards, not adhering to the body; no contractile vacuole; protoplasm granular; movement a smooth rapid gliding without any vibration (Plate III., Fig. 14). Cysts (Plate I., Fig. 19) polyhedral (generally roughly hexagonal in optical section) with a thick outer wall without any aperture; protoplasmic contents spherical and lying freely inside, containing a large rather refringent mass and generally a number of smaller granules, diameter 8 to 9μ.

This species is also very widely distributed, having been found in 78 of the soils examined. Allison found it in 45 per cent. of his American soils.

Phyllomonas contorta, Klebs.—Shape flattened, triangular and twisted, not amœboid; length 6 to 7μ; flagellum slightly longer than the body, arising

at the anterior apex and directed backwards; contractile vacuole in the broad hinder end.

Wolff describes it from a field soil.*

Family (iv.) *Trypanosomaceæ.*

Proleptomonas fæcicola, Woodcock.—This is the only member of this family that has been found living freely in soil. A narrow spindle-shaped, perfectly straight and rigid organism about 7 to 8 μ long and with a single flagellum about twice as long as the body inserted at the extreme anterior tip (though actually arising from a granule just in front of the nucleus which is near the middle of the body) and directed straight forwards. The movements are quite unmistakable, for it darts forwards in a straight line with a spiral movement so rapid that the tip of the body appears blurred like the tip of a vibrating tuning-fork; at times it darts backwards for a short distance and then again resumes its forward motion. First described by Woodcock from the dung of farm animals. It is, however, also widely distributed in soils, having been found in 17 of the 148 soils, including those from localities as different as Greenland and Spitsbergen on the one hand, and India, Sudan, and Argentine on the other. No other observers have recorded it, but Fantham and Taylor [36] record a species which they name *Herpetomonas terricola*, but of which they seem to have published

* Recently a flagellate apparently belonging to the genus *Cryptobia* Leidy (= *Trypanoplasma*, Lav. and Mesnil) has been found in New York soils by Dr F. O. Holmes, and by myself in soils from New Jersey and Utah, and in fermenting straw at Rothamsted A description will be published shortly.

no definition, and which one may assume to have been identical with the present species.

Family (v.) *Amphimonadaceæ.—Mostly ovoid to spherical with two equal flagella both directed forwards: either free or enclosed in a gelatinous sheath.*

Spongomonas sp. Stein. — Diameter 5 to 6 μ; shape spherical to broadly elliptical, rather flattened; flagella about two to three times body length; usually found inside a gelatinous capsule the surface of which is encrusted with cocci; the flagella protrude and throw the whole organism and its sheath into a very rapid quivering by their activity. The motion of the flagella is so rapid that they cannot be seen, but any cocci which are near enough are whirled downwards with a circling motion to the base of the flagella. The gelatinous sheaths often unite into a considerable mass in which a number of the flagellates are embedded, and in this condition they resemble a mass of small *Phalansterium solitarium* (Francé[42] in fact regards the Phalansteriaceæ as closely related to the Spongomonadinæ). Free-swimming individuals also occur and swim quickly in straight lines, turning on the long axis as they do so. This rotary motion combined with their flattened shape gives a curious flickering appearance to the swimming organism. The contractile vacuole is single and near the posterior end. Nutrition saprophytic.[72]

This form is quite common in soils, having been found in 34 of the 148 examined, but its specific identity has not yet been determined. In size

and general appearance it is very like *S. minima*, Dangeard.[28]

Cladomonas sp. Stein.—Very like *Spongomonas* but the gelatinous sheaths grow out into long branching tubes, with a flagellate embedded at the end of each branch. It has only once been recorded in soil, namely, from a Spitsbergen sample.

Family (vi.) *Tetramitaceæ.—Free-swimming flagellates with four to six flagella.* Only one genus, *Tetramitus*, is found in the soil.

Tetramitus rostratus, Perty. A large flagellate 18 to 30 μ long, more or less triangular in shape, being tapering and pointed behind and squarely truncated in front with a lip projecting laterally from one side of the anterior end; flagella in two pairs (one pair longer than the other) all directed forwards; contractile vacuole large and situated at the anterior end (Plate II., Fig. 12). Bunting[14] has stated that this organism at times loses the flagella completely and becomes an amœba of the limax type, but this has not been observed in any of our cultures.

Common in dirty waters, septic tanks of sewage works, etc., and found in soils from Kenia, Gough Island, Tristan da Cunha, and India (Pusa and Coimbatore). Allison found it in 15 per cent. of his American soils.

T. spiralis, Goodey.—More or less pyriform in shape but somewhat pointed at each end and with a longitudinal spiral groove; in old cultures very narrow elongated forms appear which can easily be mistaken for *Spiromonas angusta*. The flagella are arranged

in two pairs, the members of which are often so closely applied to one another that they appear as a single flagellum and their double nature can then only be recognised with difficulty. The shorter pair is directed forwards, while the other pair (usually more than twice as long as the body) lies in the spiral groove and trails behind the body. The movements are rapid and spiral; length 8 to 12 μ.

The cysts are extremely characteristic. A typical well-formed specimen has eight pentagonal faces with the edges between them raised to form ridges so that as the cyst is gently rolled over on the microscope slide it gives the successive appearances shown in Plate I., Figs. 9, 10, 11. Cysts with six rectangular faces (Plate I., Fig. 12) are also fairly often seen though they are not as common as the pentagonal forms. The outer wall is colourless and transparent and the protoplasmic contents lie freely inside as a rounded, finely vacuolated, non-granular mass. The shortest diameter of the cysts averages about 5 to 6 μ.

This species was first described by Goodey[52] from some old Rothamsted soils and does not seem to have been found in any other habitat except soil. It has been found in 42 of the 148 samples examined here. Perey found it in all 5 of the French soils she examined, and Allison in 75 per cent. of his American soils.

T. pyriformis, Klebs.—An ovoid form, pointed behind, with four equal flagella of which three are directed forwards and one backwards; found in a single soil from Gough Island.

Fellers and Allison record *T. variabilis*, Stokes, as occurring rarely in soil. They describe it as 10 to 20 μ long, with four subequal flagella (all directed forwards in their diagram); body obovate, plastic and variable in shape.

Yakimoff and Zérèn also record an unidentified species of *Tetramitus* in one of the soils they examined.

The genera *Oikomonas* and *Monas* are often included in this Order but are more correctly grouped with the Chrysomonadinæ on account of the structure and mode of formation of the cysts.

ORDER 3.—DISTOMATINÆ. FLAGELLATES VERY LIKE THE PROTOMASTIGINÆ, BUT BILATERALLY SYMMETRICAL, HAVING TWO MOUTH OPENINGS AND FOUR OR MORE FLAGELLA ARRANGED IN TWO GROUPS. NUTRITION BOTH HOLOZOIC AND SAPROPHYTIC.

Hexamitus inflatus, Duj.—Shape oval, truncated behind; length 13 to 25 μ, width 9 to 15 μ; flagella in two groups of four each, of which three are directed forwards and one backwards. Recorded only by Fellers and Allison.

Spironema multiciliata, Klebs. — In this the bilateral arrangement is not obvious. A very elongated form tapering to a fine point behind and rounded in front; length 20 to 25 μ, width about 4 μ; flagella short, numerous (7 to 18), and arranged in two rows (not necessarily with the same number in each) at the anterior end of the body.

Goodey [52] found this curious flagellate in a sample of Rothamsted soil that had been stored since 1865, and it has also been found in a single sample from Argentine.

The remaining Orders are those which are commonly called the *Phytoflagellates* owing to the fact that the typical members possess chromatophores. In all the Orders, however, colourless species without chromatophores are included, and it is mainly these which are found in the soil, though some coloured forms also occur. A further distinction between the Phytoflagellates and the three preceding Orders is that whereas in all the former, except in the Chrysomonads, the metabolic products are generally starch, paramylon, leucosin, etc., in the latter they take the form of oily globules.

ORDER 4. — CHRYSOMONADINÆ. SMALL FLAGELLATES WHICH WHEN NOT POSSESSING CHROMATOPHORES RESEMBLE THE PROTOMASTIGINÆ CLOSELY. CUTICLE GENERALLY PRESENT BUT SO THIN THAT IT DOES NOT PREVENT THEM FROM BECOMING AMŒBOID AT TIMES. ONE OR TWO FLAGELLA AT THE ANTERIOR END. CYST-FORMATION ENDOGENOUS, THE CYST WALL GENERALLY MORE OR LESS IMPREGNATED WITH SILICA AND PERFORATED BY A LARGE PORE STOPPED BY A PLUG.

These are mostly planktonic forms which avoid contaminated waters and so are naturally not represented by many species in the soil, and of the three Sub-Orders into which the Order is divided, only one, the Euchrysomonadinæ is found. Nutrition partly holophytic and partly holozoic. The soil forms, being colourless, are presumably entirely holozoic.

Family (i.) *Euchromulinaceæ*, Pascher: *forms with a single flagellum, a simple vacuole system, and without any ornate sheath.*

Oikomonas, S. Kent (*Chromulina*, Cienkowsky;

Heterochromulina, Pascher). — Small, more or less spherical flagellates, sometimes pointed or stalked behind, somewhat amœboid. Unlike the majority of the Chrysomonads, *Oikomonas* is rather characteristic of very dirty and putrifying waters. Many species are also marine. Most of the *Oikomonads* possess chromatophores and combine holozoic and holophytic modes of nutrition. The common soil species is colourless and its mode of nutrition, though presumably holozoic, has not been fully investigated.

O. termo (Ehrbg.) Martin.—Diameter 4 to 5 μ; typically spherical but sometimes elongated; flagellum about equal to the length of the body and held apparently stiffly in front; contractile vacuole single and situated at the base of the flagellum; swims freely in smooth curves without any jerky or vibratory movement (Plate II., Figs. 5, 6). Conjugation occurs in old cultures giving rise to very large individuals which continue to swim about for some time before encysting. Cysts spherical, with a single pore; wall smooth and colourless but (unlike that of *Heteromita* cysts) appearing as a thick black line in optical section.

These cysts, which are very characteristic and occur in cultures in large numbers, differ somewhat from the figures given by Martin,[76] who appears to have drawn only the immature forms (Plate I., Figs. 17, 18). The process of cyst-formation also differs considerably from that described for closely-related species by Scherffel,[107, 108], Doflein,[32] and Pascher.[89] According to these investigators encystment in the Chrysomonadinæ is endogenous, the cyst being formed inside the body of the organism and the external protoplasm being absorbed into it through a hole which ultimately becomes the pore of the cyst. The earlier stages of encystment in *O. termo* agree closely with this, for a spherical mass

of protoplasm becomes separated off within the body of a rather large individual, presumably a zygote, though no cytological observations were made to confirm this (Plate I., Fig. 13). But instead of this inner mass becoming surrounded by a firm wall (the ultimate cyst wall) it develops a vacuole at its centre which enlarges and presses the inner mass against the surrounding protoplasm which by this time has become a hollow, hyaline sphere (Plate I., Figs. 14, 15). The endogenous mass thus becomes simply a thin lining to the outer sphere, the periphery of which becomes the cyst wall. Though this process has not been followed in stained preparations, there is in the earlier stages a relatively large refringent body in the inner mass which is presumably the nucleus, and in the penultimate stage this is still visible as a slight thickening of the lining at one place (Fig. 16). The form of the nucleus in the mature cyst, however, has not been observed owing to the failure of the stains used to penetrate the wall.

With the exception of *Heteromita globosa* this is the most abundant and widely distributed of all soil flagellates and there are few soils in which it cannot be found.

O. mutabilis, Kent.—A rather larger form, often with a stalk at the posterior end; flagellum about twice the body length; contractile vacuoles two, posterior. Fellers and Allison (common), Yakimoff and Zérèn (in 7 out of 15 soils). Cunningham and Löhnis record *O. dallingeri*, Kent, but it is rather doubtful to what organism this refers.

Oikomonas granulata, Yakimoff, Solowzoff, and Wassielewsky.[125] — A slowly-swimming, ovoid to spherical flagellate with a long flagellum which arises at the anterior pole and is directed forwards at the base, but then curves backwards so that the greater part of it trails behind. The nucleus lies in front of the middle, and at one side of the body are three to

twelve refringent granules. The size is not stated. This species was first found in the stools of three dysenteric patients, and later in the intestine of white mice, and finally by Yakimoff and Zérèn in 3 out of 15 Russian soils. The description given is, however, too inadequate for identification to be possible and no other soil investigators have described any organism that seems to be identical with it.

Chrysamœba radians, Klebs.—A large egg-shaped organism about 15 μ long with two chromatophores and three contractile vacuoles. It has an amœboid form in which it has long radiating pointed pseudopodia and in this stage may form gelatinous colonies.

Fantham and Paterson from two localities in South Africa.

Family (ii.) *Mallomonadaceæ.—Forms with a thick periplast and a complicated vacuole system.*

Mallomonas, Perty. — Fairly large flagellates, mostly spindle-shaped, enclosed in siliceous plates, and with a number of long fine siliceous needles at one or both ends. Flagellum single. This is a typical planktonic genus, but some species are regarded as occurring typically in waters rich in dissolved or suspended humus. Fellers and Allison gave a doubtful record of the occurrence of an unidentified species of it in soil; length 12 to 28 μ; shape ovoid, rounded behind and tapering to a blunt point at the anterior end.

Family (iii.) *Euochromonadaceæ.*—*Forms with one main flagellum and one or two shorter accessory flagella: simple contractile vacuole at anterior end: cuticle very thin: solitary or colonial.*

Monas (Ehrbg.) Stein. (*Ochromonas*, Wyssotzki, *Heterochromonas*, Pascher).—Very like *Oikomonas* but having one or sometimes two short accessory flagella at the base of the principal flagellum. There is a thickened area ("Mundstrich" of the German authors) of unknown function at the base of the flagella.

This genus is commonly found in water containing much organic matter, and Alexeieff[2] writes of them: "Les Monas sont des Flagellés qui présentent une ubiquité avec laquelle seules les espèces du genre *Bodo* pourraient rivaliser. Il n'y a pas une infusion où à un certain moment on ne trouve des représentants du genre Monas." One would therefore expect to find this genus commonly present in the soil, and many soil investigators have indeed recorded one or both of the following species as being very abundant in soils, but with the exception of Fellers and Allison, Cunningham and Löhnis, and Yakimoff and Zérèn, these observers have all overlooked the common *Oikomonas termo*, and consequently it seems probable that many if not most of these records are faulty identifications of this organism. In this laboratory for a time the real nature of the large zygotes of *Oikomonas* was not recognised and they were regarded as belonging to some species of *Monas*, and it seems not improbable that others have fallen into the same mistake.

Monas guttula, Ehrbg.—Spherical to ovate or pyriform; length about 10 μ; main flagellum rather longer than the body, with two very short accessory flagella; contractile vacuole mid-lateral; no eye-spot; usually attached to some solid object by a posterior thread. Scarce in Rothamsted soils.

Wolff, Cunningham and Löhnis, Koch, Waksman, Fellers and Allison, Nowikoff, Yakimoff and Zérèn record it.

Organisms probably belonging to this species were also found in soils from Antigua, Tristan da Cunha, Mauritius (5 samples) and Natal.

M. vivipara, Ehrbg.—A large species; length 20 to 40 μ; spherical to egg-shaped; main flagellum $1\frac{1}{2}$ times body length, two short accessory flagella; contractile vacuole mid-lateral, stigma and "Mundstrich" both present; cell very granular.

Wolff, Cunningham and Löhnis, Koch, Waksman, Fellers and Allison, Nowikoff record it.

Sherman has also recorded *Monas* sp.

Cephalothamnion cyclopum, Stein.—More or less wedge-shaped, the anterior end being truncated and drawn out to a lip at one side, and the posterior end being pointed and often drawn out to a stalk by which the organism attaches itself; length 5 to 10 μ; main flagellum equal to body length; one accessory flagellum about half as long; contractile vacuole anterior; often colonial.

Tristan da Cunha, Mauritius, Argentine and India (Punjab).

Physomonas elongata, Stokes.—A form very like

Actinomonas, but differing in having a short accessory flagellum and a "Mundstrich."

Fellers and Allison (occasional).

Polypseudopodius bacterioides, Pusch.—An elongated spindle-shaped organism like a large bacterium; length about 4 to 5 μ, with two flagella inserted at the anterior end, one slightly longer than the body and the other about half as long; movements active and extraordinarily erratic. An amœboid phase is also known. The affinities of this flagellate are doubtful, but it is probably closely related to the Monads.

One of the organisms obtained by Puschkarew from the air which Martin and Lewin [78] state can all be found in the soil.

ORDER 5.—CRYPTOMONADINÆ. RATHER SMALL FORMS WITH TWO FLAGELLA, USUALLY EQUAL, ARISING JUST BEHIND THE ANTERIOR END IN A HOLLOW WHICH IS USUALLY THE OPENING OF A FUNNEL WHICH RUNS DEEP INTO THE INTERIOR OF THE CELL. BODY ENCLOSED IN A MEMBRANE AND CONSEQUENTLY NOT AMŒBOID. SHAPE TYPICALLY EGG-LIKE AND MORE OR LESS FLATTENED. ONE OR TWO SIMPLE CONTRACTILE VACUOLES AT THE ANTERIOR END.

The majority of species in this Order are marine. The non-marine species usually occur in waters containing plenty of organic matter, but are nevertheless comparatively scarce in soil.

Chilomonas paramœcium, Ehrbg.—Length 20 to 40 μ, anterior end obliquely truncated, hind end somewhat tapering and rounded and often slightly curved. Flagella unequal, the longer one being

about equal to the body length. Cytopharynx and periplast both well developed. Usually containing many starch grains. Contractile vacuole single, anterior. Nucleus just behind middle of body. Nutrition saprophytic.

In a single soil from Antigua. Wolff, Fellers and Allison (occasional), Fantham and Paterson once only, and Yakimoff and Zérèn (in 8 out of 15 soils). Fellers and Allison also record what was possibly another species of the same genus.

Cryptomonas, Ehrbg.—Very similar to *Chilomonas*, but containing chlorophyll. Spitsbergen (?*C. obovoides*).

Fellers and Allison found *C. ovata* occasionally in New Jersey soils, and Yakimoff and Zérèn found what was probably the same species occasionally in their Russian soils.

Cyathomonas truncata, Ehrbg.—A colourless form differing from *Cryptomonas* in containing oil globules instead of starch grains. Length 15 to 30 μ, laterally compressed, but in side view nearly as broad as long and with obliquely truncated ends. The cytopharynx is surrounded with a ring of strongly refractile bodies.

Nutrition holozoic. Recorded from the soil only by Cunningham and Löhnis.

Rhodomonas sp.—A form containing a red pigment and with the cytopharynx less developed than in the other members of this Order.

Found in a single South African soil by Fantham and Paterson.

ORDER 6.—EUGLENINÆ. FORMS WITH ONE OR TWO FLAGELLA: ENCLOSED IN A MEMBRANE BUT OFTEN SOMEWHAT METABOLIC THOUGH NEVER AMŒBOID: MOSTLY WITH GREEN CHROMATOPHORES, AND WITH PARAMYLUM AND OIL AS THE MAIN ASSIMILATION PRODUCTS. THE MOST CHARACTERISTIC FEATURE IS THE COMPLICATED VACUOLE SYSTEM SITUATED AT THE ANTERIOR END AND CONSISTING OF ONE OR MORE ACCESSORY VACUOLES USUALLY FORMED BY THE COALESCENCE OF A NUMBER OF SMALLER VACUOLES WHICH IN CONTRACTING EMPTY THEIR CONTENTS INTO A LARGE MAIN VACUOLE OR RESERVOIR WHICH IN TURN COMMUNICATES WITH THE CYTOPHARYNX.

These forms are especially abundant in waters containing plenty of decaying organic matter and are represented by a considerable number of species in the soil, though none of them seems to attain very high numbers. Members of some genera are known to ingest bacteria, but most of the soil forms are mainly saprophytic.

Family (i.) *Euglenaceæ.—Not bilaterally symmetrical: division occurs in the resting stage.*

Euglena, Ehrbg.—Large, more or less elongated, flexible and rather metabolic forms with a thick and usually spirally marked cuticle; flagellum single, arising in the cytopharynx; chromatophores present; stigma usually present.

Dr Bristol Roach has found this organism in Rothamsted soils, but owing to its slow development in cultures (especially when kept in a darkened incubator) it has not been found in the course of the present investigations. The following species have been recorded by other observers.

E. acus, Ehrbg.—Size 140 to 180 μ × 10 μ, hind end pointed; only slightly metabolic; flagellum about half the body length; chromatophores numerous and disc-shaped; no pyrenoid.

Fellers and Allison (in a rich black forest soil, length 40 to 100 μ), Nowikoff.

E. deses, Ehrbg.—Size 85 to 155 μ × 15 to 22 μ, very metabolic; flagellum short; chromatophores as in *E. acus*; pyrenoid present.

Fantham and Paterson (in several South African soils).

E. oxyuris, Schmarda.—Size 375 to 490 μ × 30 μ to 45 μ; with strong spiral markings; only slightly metabolic; somewhat flattened; flagellum half the body length; numerous disc-shaped chromatophores; pyrenoid absent but two ring-shaped paramylum masses lie one behind and the other in front of the nucleus. Fantham and Taylor, Fantham and Paterson.

E. spirogyra, Ehrbg.—Size 80 μ × 8 μ; feebly metabolic; hind-end drawn out to a pointed tail; membrane with spiral rows of minute knobs; chromatophores numerous, disc-shaped; no pyrenoids; rings of paramylum much as in *E. oxyuris*.

Fantham and Taylor, Fantham and Paterson (from one soil only in each case).

E. velata, Klebs.—A broader, ovoid form about 100 μ long by 25 to 30 μ broad; flagellum nearly as long as the body; numerous star-shaped chromatophores; pyrenoids enclosed in a double wall.

Francé.

E. viridis, Ehrbg.—A very metabolic, spindle-

shaped form, 52 to 57 μ long by 14 to 18 μ wide; flagellum about equal to the body; chromatophore single, star-shaped, and situated in front of the nucleus; pyrenoid present and surrounded by grains of paramylum.

Wolff, Waksman, Fellers and Allison, Fantham and Taylor, Fantham and Paterson and Nowikoff. The specimens found by Fellers and Allison range between 18 μ and 60 μ in length. Fantham and Taylor[36] regard it as a characteristic spring (*i.e.* September) form in the Karroo, but this seasonal incidence does not appear to have been noticed elsewhere.

Unidentified species of *Euglena* have also been found in soils by Lodge and Smith and by Koch.

Eutreptia viridis, Perty.—A spindle-shaped form about 49 to 66 μ long by 3 to 15 μ broad, very metabolic, with two equal flagella; chromatophores disc-shaped; no pyrenoids; stigma present.

Fellers and Allison mention an organism which they tentatively record as belonging to this species.

Phacus, Duj.—Somewhat like *Euglena* but with a firm membrane; shape asymmetrical and flattened, usually round or oval and pointed behind. Chromatophores disc-shaped.

P. longicaudus (Ehrbg.), Duj.—An oval form with a long caudal process, membrane with longitudinal stripes; length 85 to 115 μ, width 46 to 70 μ. Fellers and Allison (rare), Fantham and Paterson (in a single water-logged soil).

P. pyrum (Ehrbg.), Stein.—Like *P. longicaudus*

but smaller (length 30 to 55 μ) and with spiral stripes on the membrane.

Fellers and Allison (occasional). Yakimoff and Zérèn (in one soil only).

Trachelomonas volvocina, Ehrbg.—A uniflagellate form distinguished from *Euglena*, etc., by being enclosed in a spherical outer sheath or lorica; diameter 25 to 50 μ.

Fellers and Allison (occasional).

Cryptoglena pigra, Ehrbg.—Also uniflagellate, ovoid, enclosed in a double, thin, but rigid test; two large lateral chloroplasts; stigma present; size 11 to 15 μ × 6 to 9.5 μ.

Fellers and Allison (occasional).

Family (ii.) *Astasiaceæ.—Similar to the Euglenaceæ but having no chromatophores: division in the active stage.*

Astasia, Duj.—Very metabolic, moving with an amœboid creeping movement or swimming with a rotary action; one flagellum.

Fellers and Allison tentatively identify an organism found occasionally by them as being *A. trichophora*, Ehrbg., but this species is not recognised as a valid one by Lemmermann. Their organism was 30 to 60 μ long, plastic with transparent endoplasm and no eye-spot.

Astasia sp. has also been recorded by Martin (sick soils), Fellers and Allison, and Nowikoff.

Distigma (*Astasia*) *proteus* (Ehrbg.).—A long, spindle-shaped flagellate; length 46 to 110 μ. Two

flagella, one about half the body length directed forwards, and the other much shorter and turned backwards. Movements like those of *Astasia*.

Francé, Yakimoff and Zérèn (in 6 out of 15 soils).

Clostenema (*Sphenomonas*) *socialis*, Stokes.—Differs from *Distigma* in being rigid, and in its movement which is a gliding forwards in the direction of the long flagellum; length about 8 to 12 μ (Conn [20]).

A single doubtful record by Fellers and Allison.

Menoidium, Perty.—An elongated, banana-shaped flagellate, squarely truncated at the anterior end, circular in section but with about six longitudinal ridges; shape quite rigid; length 15 to 18 μ; flagellum single and equal to about 2/3 of the body length; protoplasm clear and glassy with some granules at the anterior end; swims rapidly and in a straight line turning on the long axis.

This organism (probably *M. incurvum* (Fres), Klebs) was found in a Gough Island soil. A very similar but broader and more fusiform flagellate (size 19 μ × 9 μ) was found in a soil from Mauritius.

Family (iii.) *Peranemaceæ.—More or less bilaterally symmetrical forms without chromatophores.* Characteristic of water containing decaying organic matter.

Nutrition partly holozoic, partly saprophytic.

Petalomonas, Stein.—Rigid, usually flattened, and markedly asymmetrical, with a single stout flagellum directed forwards, of which only the distal end generally moves.

P. angusta (Klebs), Lemm.—A narrow ovoid form with a longitudinal groove on the ventral surface; flagellum about equal to the body length; length 8 to 12 μ (14 to 23 μ, Lemmermann[71]).

Tristan da Cunha.

P. mediocanellata, Stein.—Very like *P. angusta* but with both dorsal and ventral surfaces grooved.

Greenland: also recorded by Francé and (?) Fellers and Allison (rare).

P. pleurosigma, Stokes.—Probably only a variety of the last species. Found in 3 South African soils by Fantham and Taylor and Fantham and Paterson.

Scytomonas, Stein (= *Copromonas*, Dobell).—Very like *Petalomonas* but not flattened.

S. pusilla, Stein (= *Copromonas subtilis*, Dobell[29]). —Shape ovoid, narrowing in front; length 8 to 15 μ; flagellum slightly longer than the body (Plate IV., Fig. 14). Found in various soils from England, Egypt, Palestine, Mauritius, and Argentine. Similar forms probably belonging to the same species have been found in soils from Santa Lucia, Ocean Island, Natal, Serbia, and Spitsbergen, and by Martin (sick soils) and Perey (French soils).

According to Alexeieff[1] this species is particularly characteristic of putrefying infusions.

Peranema trichophorum (Ehrbg.), Stein.—Very metabolic, with a rod-like organ behind the cytopharynx; more or less spindle-shaped; length 22 to 70 μ; flagellum 1 to 1½ times the body length; cell-membrane with spiral striations. Wolff (field soils), (?) Koch (greenhouse soils), Fellers and Allison

(occasional; length 50 to 120 μ), Fantham and Taylor, Fantham and Paterson (widely distributed in soils both cultivated and uncultivated, water-logged and not water-logged), Yakimoff and Zérèn (in 2 out of 15 soils). Fantham and Taylor mention it as an autumn (*i.e.* April) form in the Karroo. Nowikoff also records *Peranema* sp.

Urceolus cyclostomus (Stein), Meresch. — Differs from *Peranema* in having a large funnel-shaped oral aperture in which the flagellum is inserted; size 26 to 50 μ × 17 to 30 μ.

Found in one soil only by Fantham and Paterson.

Anisonema minus, Sandon. — A flattened, egg-shaped flagellate, narrower and slightly asymmetrical in front, with a longitudinal groove on the lower surface; not metabolic; two flagella, the stouter one about equal to the body length, directed forwards, the other more slender and about twice as long, trailed passively behind; length 6 to 9 μ; movements slow and very steady.

A very widely distributed species, having been found in soils from Spitsbergen, West Indies, Cape Verde Island, St Paul's Rock, Gough Island, Nauru, Ocean Island, (?) Mauritius, Argentine, Japan, Australia, India, and South Africa.

Entosiphon sulcatum (Duj.), Stein (*Anisonema sulcatum*, Duj.).—Flattened, ovoid; not metabolic; size about 20 to 25 μ × 10 to 15 μ but often smaller; two flagella much as in *Anisonema*; with a long rod-like organ extending from the base of the flagella almost to the posterior end of the body (Plate IV., Fig. 13).

St Helena, Tristan da Cunha, Ocean Island, and India (Coimbatore). Goodey, Fantham and Taylor, and Fantham and Paterson.

Heteronema acus (Ehrbg.), Stein.—Another biflagellate form but not flattened; spindle-shaped with rounded ends; metabolic; length 35 to 80 μ; anterior flagellum slightly longer than the body; trailing flagellum only about half as long.

Nutrition holozoic.

Fellers and Allison (occasional), (Fellers and Allison, however, describe the *longer* flagellum as the one that is trailed). Nowikoff also records *Heteronema* sp.

ORDER 7.—PHYTOMONADINÆ. SOLITARY OR COLONIAL FORMS, ENCLOSED IN A CELLULOSE WALL: CHLOROPHYLL AND STIGMA NEARLY ALWAYS PRESENT (THE SOIL FORMS, HOWEVER, INCLUDE SEVERAL OF THE EXCEPTIONAL COLOURLESS FORMS): RESERVE MATERIAL STARCH: ONE OR MORE SIMPLE CONTRACTILE VACUOLES AT ANTERIOR END. NUTRITION IN SOIL MAINLY OR WHOLLY SAPROPHYTIC.

Family (i.) *Chlamydomonadaceæ. — Non-colonial forms with a very thin membranous envelope: two to four flagella at the anterior end, and one or two contractile vacuoles near the base of the flagella: conjugating pairs frequently observed.*

Chlamydomonas, Ehrbg.—Spherical to oval cells with two equal flagella; chromatophore single with one or more spherical or elongated pyrenoids; stigma generally present at anterior end.

Length about 12 to 30 μ. — Wolff includes *C. monadina,* Stein, among the most abundant

forms ("Leitformen") in field soils and also records *C. pulviscula*, Ehrbg., from similar soils. Waksman says that *Chlamydomonas* sp. is one of the commonest soil flagellates, and Fellers and Allison, and Yakimoff and Zérèn both record it as occasional.

Polytoma, Ehrbg.—Very like *Chlamydomonas* but colourless; the wall always retains its ellipsoidal shape but the contents often shrink and so fill only part of it; swims rapidly in a straight line rotating about the long axis. Common in water containing decaying organic matter, sewage, etc.

P. uvella, Ehrbg.—Another of Wolff's "Leitformen" in field soils. Yakimoff and Zérèn found it in 8 out of 15 soils and call it very common. Jameson[61] found it in cultures of garden soils after six to eight weeks.

In this survey *Polytoma* sp. was found in soils from Tristan da Cunha, Japan and India (Kanara) only, but probably it would have been found in more soils if the cultures had been kept longer. *Polytoma* is however a form which thrives particularly in infusions in an advanced stage of putrefaction, so possibly soil conditions are not generally the most favourable for it.

Parapolytoma satura, Jameson. — Differs from Polytoma in having the anterior end obliquely truncated, and the flagella arising in a shallower pit. Found by Jameson[61] in hay infusion cultures of garden soil after six to eight weeks.

Chlorogonium, Ehrbg. — Very thin-walled, elon-

gated, spindle-shaped, tapering behind to a fine tail; length 30 to 110 μ, maximum width about 1/5 body length; flagella two, equal, each about half the body length; chromatophore a narrow plate without pyrenoids, situated close to one side; stigma large, near middle. Found only in irrigated rice soils from Coimbatore (South India). Yakimoff and Zérèn however found *C. euchlorum*, Ehrbg., in 8 out of 15 Russian soils.

Family (ii.) *Volvocaceæ.—Cells united into colonies of definite shapes.*

Pandorina morum, Ehrbg. — Cells like *Chlamydomonas* but united into compact spherical or ellipsoidal colonies of 16 (occasionally 32) individuals. Wolff (field soils).

Possibly related to these forms is the organism previously[100] referred to as Sp. ϵ. and for which the name *Allas diplophysa* nov. gen., nov. sp. is now proposed. It is a flattened, more or less oblong organism with rounded ends, rather metabolic and sometimes with ragged pseudopodia especially at the hind end; length 10 to 24 μ, width about half the length; two flagella arising at the anterior end of the body, one, slightly longer than the body, being trailed passively behind, and the other which is very short (about 2 to 3 μ long) moving actively. The animal glides rapidly forwards very like *Allantion tachyploon*, but sometimes with a slight vibration owing to the active lashing of the short flagellum (Plate III., Fig. 15).

The preceding is a summary of the description already published to which the following observations can now be added.

Contractile vacuoles. There are two very prominent contractile vacuoles at the anterior end of the body which work independently of one another (simultaneously in some individuals, alternately in others). Two channels, one from each vacuole, open at the same spot at the base of the flagella. There is generally a slight depression here and in a few individuals the two channels have appeared to discharge into a common large vestibule at this point, but in the majority of cases no such structure has been distinguished. Small accessory vacuoles (such as are found in the majority of the Eugleninæ) are not present.

Cytology. Preparations stained with hæmatoxylin show the following features. The two flagella arise from two separate basal granules which are not connected to the nucleus by a rhizoplast, though sometimes they lie close against it (Plate IV., Fig. 1). The nucleus lies in front of the middle of the body and is of the large vesicular type with considerable peripheral chromatin. Division takes place in the resting condition when the flagella are lost, and though few dividing nuclei have been observed, the anaphase has been found in several preparations and shows a broad spindle rounded at the ends, with large polar masses not joined by a centrodesmose (Plate IV., Figs. 2-9). It is thus quite different from any stage in the nuclear division of the Eugleninæ and resembles closely the corresponding stage in some of the Phytomonadina (e.g. *Chlorogonium* (cf. [57], Plate III., Fig. 62). Fig. 3 presumably represents an early prophase and is also quite unlike that found in the Eugleninæ. Individuals containing two perfect nuclei side by side are often observed, so conjugation probably occurs but this process has not been seen in the living animals.

The systematic position of this organism is very uncertain, and further observation is required, especially on the structure of the contractile vacuoles and on the mode of nuclear division. Some individuals give the appearance of being enclosed in a very delicate cuticle like that of the Phytomonads, but attempts to demonstrate the presence of cellulose have failed and in view of the great plasticity of the organism and of its power of forming finger-like pseudopodia it seems very improbable that such a wall is generally present. At the same time the specimens which showed it had both flagella and gave no signs of being about to encyst. If this cuticle is normally present the genus will fall within the Phytomonadinæ, but the contractile vacuole system is unusual for this Order.

This species is widely distributed, having been found in 18 soils from Spitsbergen, Greenland, St Helena, West Indies, Japan, India, Mauritius, Argentine, Tristan da Cunha, and Gough Island.

Sub-Class *Dinoflagellata*.—These are distinguished from the other flagellates by being enclosed in a thick rigid cuirass or lorica, and by having two flagella, one of which lies in a transverse groove and keeps up an undulating movement, while the other lies in a longitudinal groove, and is trailed behind. The great majority of this group are planktonic (marine and fresh water) but some are parasitic. Only one, *Glenodinium pulvisculus*, Stein, has been recorded from soil. This is a relatively thin-walled, more or less spherical organism; size about $23\mu \times 18\mu$; chromatophore brownish-yellow; no stigma. It was found by Fantham and Paterson in a cultivated soil in the Transvaal.

Key to the Identification of the Soil Flagellates.

In this key each section contains the names of all the soil flagellates possessing a certain feature in common, and after each name numbers are placed referring to the other sections in which that organism occurs. Thus if an unknown flagellate is found to possess a stalk, section 33 shows that (unless it is a form not previously recorded from the soil) it must be one of the 7 species named in the section, and the references accompanying each name will probably enable all but two or three of these to be rejected with little further observation. If (as is usually the case) several features of the unknown organism can be

accurately discerned, the only genera or species that need further consideration are those which are common to all the sections concerned. Identifications should of course always be checked by reference to the descriptions given in the text and wherever possible by the use of the larger works and original papers of which the most important are given in the bibliography.

The sections of the key based on the shape of the organisms should be used with great caution (especially sections 13, 14, 15, 17, 18, 22) as in many cases this feature is very variable.

The same applies with even greater force to the sections based on movements, which are however included because in many cases they are exceedingly useful aids to identification. In fact with practice it is often quite possible to identify most of the common organisms with tolerable certainty simply by their movements.

Mastigophora.

FLAGELLA :—

(1) 1 directed forwards.

Pantostomatinæ—

Actinomonas (13, 33, 36, 53).
Mastigamœba and *Mastigella* (29, 41).

Protomastiginæ—

Codosiga (14, 15, 32, 33, 35, 47).
Monosiga (13, 14, 15, 33, 35, 47).
Salpingœca (15, 31, 33, 35).
Phalansterium (13, 14, 15, 31, 32, 35, 46, 52).
Proleptomonas (18, 45, 46).

Chrysomonadinæ—

Oikomonas (13, 14, 15, 22, 29, 48).
Chrysamœba (14, 15, 29, 31, 32, 36).
Mallomonas (14, 30, 40).

FLAGELLA—*contd.*

(1) 1 directed forwards—*contd.*

Eugleninæ (34, 40)—

Euglena (20, 22, 29, 30, 37, 39, 41).
Phacus (22, 24, 30, 37).
Trachelomonas (13, 31).
Cryptoglena (14, 31, 37, 39).
Astasia (29, 41).
Menoidium (16, 19, 30, 45).
Peranema (17, 29, 41).
Urceolus (17, 29, 41).
Petalomonas (24, 27, 30, 41).
Scytomonas (14, 30, 41).

(2) 1 directed forwards, and 1 or 2 short accessory flagella.

Chrysomonadinæ—

Monas (13, 14, 33, 39, 48).
Cephalothamnium (21, 22, 32, 33).
Physomonas (13, 33, 36).
Polypseudopodius (18, 29, 49).

(3) 1 directed backwards.

Protomastiginæ—

Sainouron (16, 29, 43, 48).
Allantion (14, 16, 30, 42).
Phyllomonas (24, 26).

(4) 1 directed backwards and an accessory flagellum.

Pantostomatinæ—

Helkesimastix, accessory flagellum very short (14, 29, 42).

Phytomonadinæ (30)—

Allas, accessory very short (14, 24, 40, 42).

Dinoflagellata (28)—

Glenodinium, accessory flagellum lies in transverse groove (13, 28).

(5) 2 equal, directed forwards.

Protomastiginæ—

Dinomonas (14, 23).
Spongomonas (13, 24, 31, 32, 45, 52).
Cladomonas (13, 31, 32, 52).

FLAGELLA—*contd.*

(5) 2 equal, directed forwards—*contd.*

Cryptomonadinæ (30, 34)—

Cryptomonas (14, 30, 34, 37).
Cyathomonas (24, 30, 34).
Rhodomonas (15, 22, 30, 34, 38).

Eugleninæ (34, 40)—

Eutreptia (18, 22, 29, 34, 37, 39, 40).

Phytomonadinæ (30)—

Chlamydomonas (13, 30, 37, 39, 45).
Polytoma (14, 30, 45, 46).
Parapolytoma (14, 30, 45).
Chlorogonium (18, 22, 30, 39).
Pandorina (30, 32, 37).

(6) 2 unequal, directed forwards.

Cryptomonadinæ (30, 34)—

Chilomonas (14, 30, 34).

(7) 2; 1 directed forwards, 1 backwards.

Pantostomatinæ—

Cercomonas, trailing flagellum adheres to the body (17, 22, 29, 41, 48).
Cercobodo, trailing flagellum does not adhere to the body: *agilis* (18, 29, 44): *vibrans* (13, 17, 29, 46).

Protomastiginæ (Bodonaceæ)—

Bodo (15, 16, 17, 22, 23, 24, 29, 44, 45, 46, 49, 51, 53).
Colponema (24, 25, 27, 53).
Heteromita (14, 15, 24, 29, 43, 48, 50).
Phyllomitus amylophagus (14).
Pleuromonas, trailing flagellum inserted at middle of body (13, 16, 29, 53).
Spiromonas (19, 26, 44).

Eugleninæ (34, 40)—

Distigma (*Astasia*) *proteus* (18, 29, 41).
Clostenema (18, 30, 42).
Heteronema (17, 29).
Anisonema (24, 27, 30, 41).
Entosiphon (24, 30).

FLAGELLA—*contd.*

(8) 2; both directed backwards.
Protomastiginæ—
Phyllomitus undulans (proximal parts of flagella united) (14).

(9) 4; 2 directed forwards and 2 backwards.
Protomastiginæ—
Tetramitus spiralis (15, 18, 20, 26, 44).

(10) 4; directed forwards.
Protomastiginæ—
Tetramitus spp. (except *T. spiralis*) (15, 21, 22, 29).

(11) 8; 6 directed forwards and 2 backwards.
Distomatinæ (25)—
Hexamitus (14, 25.)

(12) Many.
Distomatinæ (25)—
Spironema (20, 22, 25).

SHAPE:—

(13) Spherical.
Pantostomatinæ—
Cercobodo vibrans (7, 17, 29, 46).
Actinomonas (1, 33, 36, 53).
Protomastiginæ—
Monosiga (1, 14, 15, 33, 35, 47).
Phalansterium (1, 14, 15, 31, 32, 35, 46, 52).
Pleuromonas (7, 16, 29, 53).
Spongomonas, slightly flattened (5, 24, 31, 32, 45, 52).
Cladomonas, slightly flattened (5, 31, 32, 52).
Chrysomonadinæ—
Oikomonas, shape variable (1, 14, 15, 22, 29, 48).
Monas, shape variable (2, 14, 33, 39, 48).
Physomonas (2, 33, 36).
Eugleninæ (34, 40)—
Trachelomonas (1, 31).
Phytomonadinæ (30)—
Chlamydomonas (5, 30, 37, 39, 45).
Dinoflagellata (28)—
Glenodinium (4, 28).

Shape—*contd.*

(14) Ovoid ellipsoidal (oval or elliptical if flattened).

Pantostomatinæ—

Helkesimastix (4, 29, 42).

Protomastiginæ—

Codosiga (1, 15, 32, 33, 35, 47).

Monosiga (1, 13, 15, 33, 35, 47).

Phalansterium (1, 13, 15, 31, 32, 35, 46, 52).

Dinomonas (5, 23).

Heteromita spp. (7, 15, 24, 29, 43, 48, 50).

Phyllomitus (7, 8).

Allantion (3, 16, 30, 42).

Distomatinæ (25)—

Hexamitus, broad, truncated behind (11, 25).

Phytomonadinæ—

Allas (4, 24, 40, 42).

Polytoma (5, 30, 45, 46).

Parapolytoma (5, 30, 45).

Chrysomonadinæ—

Oikomonas (1, 13, 15, 22, 29, 48).

Chrysamœba, shape variable (1, 15, 29, 31, 32, 36)

Mallomonas (1, 30, 40).

Monas (2, 13, 33, 39, 48).

Cryptomonadinæ (30, 34)—

Chilomonas, truncated in front (6, 30, 34).

Cryptomonas (5, 30, 34, 37).

Eugleninæ (34, 40)—

Cryptoglena (1, 31, 37, 39).

Scytomonas (1, 30, 41).

(15) Pear-shaped, broader end generally in front.

Protomastiginæ—

Codosiga (1, 14, 32, 33, 35, 47).

Monosiga (1, 13, 14, 33, 35, 47).

Salpingœca (1, 31, 33, 35).

Phalansterium, free-swimming stage, narrow end in front (1, 13, 14, 31, 32, 35, 46, 52).

Bodo edax, narrower end in front (7, 23, 29, 46).

„ *celer* „ „ „ (7, 23, 29, 45, 49).

Heteromita globosa (7, 29, 43).

SHAPE—*contd.*

(15) Pear-shaped, broader end generally in front—*contd.*

Protomastiginæ—*contd.*

Tetramitus spiralis, sometimes very elongated (9, 18, 20, 26, 44).

Tetramitus pyriformis (10).

Chrysomonadinæ—

Oikomonas (1, 13, 14, 22, 29, 48).

Rhodomonas (5, 22, 30, 34, 38).

Chrysomœba (1, 14, 29, 31, 32, 36).

(16) Crescentic.

Protomastiginæ—

Bodo saltans, bean-shaped (7, 29, 44, 53).

Pleuromonas, bean-shaped to spherical (7, 13, 29, 53).

Sainouron, generally somewhat tapering behind (3, 29, 43, 48).

Allantion, sometimes (3, 14, 30, 42).

Eugleninæ (34, 40)—

Menoidium, banana-shaped (1, 19, 30, 45).

(17) Spindle-shaped, broad.

Pantostomatinæ—

Cercomonas, very variable (7, 22, 29, 41, 48).

Cercobodo vibrans, or spherical to ovoid (7, 13, 29, 46).

Protomastiginæ—

Bodo terricola, ends rounded (7, 29, 51).

Eugleninæ (34, 40)—

Peranema (1, 29, 41).

Urceolus, anterior extremity expanded (1, 29, 41).

Heteronema, ends rounded (7, 29).

(18) Spindle-shaped, narrow.

Pantostomatinæ—

Cercobodo agilis, very variable (7, 29, 44).

Protomastiginæ—

Proleptomonas (1, 45, 46).

Tetramitus spiralis, sometimes (9, 15, 20, 26, 44).

Chrysomonadinæ—

Polypseudopodius, very variable (2, 29, 49).

Eugleninæ (34, 40)—

Eutreptia, anterior end rounded, posterior end tapering (5, 22, 29, 34, 37, 39, 40).

SHAPE—*contd.*

(18) Spindle-shaped, narrow—*contd.*

Eugleninæ—*contd.*

Distigma (7, 29, 41).

Clostenema (7, 30, 42).

Phytomonadinæ—

Chlorogonium (5, 22, 30, 39).

(19) Elongated, both ends rounded—

Protomastiginæ—

Spiromonas (7, 26, 44).

Eugleninæ (34, 40).

Menoidium, generally curved (1, 16, 30, 45).

(20) Elongated, anterior end rounded, posterior end tapering.

Protomastiginæ—

Tetramitus spiralis, sometimes (9, 15, 18, 26, 44).

Distomatinæ (25)—

Spironema (12, 22, 25).

Eugleninæ (34, 40)—

Euglena (1, 22, 29, 30, 37, 39, 41).

(21) Conical or wedge-shaped, broad end in front.

Protomastiginæ—

Tetramitus rostratus (10, 22, 29, 44).

Chrysomonadinæ—

Cephalothamnium (2, 22, 32, 33).

(22) Hind end tapering to a point.

All sections (20, 21).

Pantostomatinæ—

Cercomonas, generally (7, 17, 29, 41, 48).

Protomastiginæ—

Bodo caudatus, very polymorphic (7, 24, 29, 49).

Tetramitus rostratus, generally (10, 21, 29, 44).

Distomatinæ (25)—

Spironema (12, 20, 25).

Chrysomonadinæ—

Oikomonas, occasionally (1, 13, 14, 15, 29, 48).

Cephalothamnium (2, 21, 32, 33).

Cryptomonadinæ (34, 40)—

Rhodomonas, sometimes (5, 15, 30, 34, 38).

Eugleninæ (34, 40)—

Euglena (1, 20, 29, 30, 37, 39, 41).

SHAPE—*contd.*

(22) Hind end tapering to a point—*contd.*

Eugleninæ—*contd.*

Eutreptia (5, 18, 29, 34, 37, 39, 40).

Phacus (1, 24, 30, 37).

Phytomonadinæ—

Chlorogonium (5, 18, 30, 39).

(23) Anterior end tapering to form a beak.

Protomastiginæ—

Bodo edax (7, 15, 29, 46).

„ *celer* (7, 15, 29, 45, 49).

Dinomonas (5, 14).

(24) Cell flattened.

Protomastiginæ—

Bodo caudatus, leaf-like and very polymorphic (7, 22, 29, 49).

Colponema, elliptical (7, 25, 27, 53).

Heteromita compressus, oval (7, 29).

„ *ovatus* „ (7, 29, 50).

Phyllomonas, leaf-like, triangular (3, 26).

Spongomonas, round, flattening not very pronounced (5, 13, 31, 32, 45, 52).

Cryptomonadinæ—

Cyathomonas, broad, ends obliquely truncated (5, 30, 34).

Eugleninæ (34, 40)—

Phacus, asymmetrical (1, 22, 30, 37).

Petalomonas (1, 27, 30, 41).

Anisonema (7, 27, 30, 41).

Entosiphon (7, 30).

Phytomonadinæ ?—

Allas (4, 14, 40, 42).

(25) Cell bilaterally symmetrical.

Protomastiginæ—

Colponema (7, 24, 27, 53).

Distomatinæ (25)—

Hexamitus (11, 14).

Spironema, symmetry not obvious (12, 20, 22).

Eugleninæ (the Peranemaceæ are mostly more or less bilaterally symmetrical (34, 40).

SHAPE—*contd.*

(26) Cell twisted.

Protomastiginæ—

Spiromonas (7, 19, 44).
Phyllomonas (3, 24).
Tetramitus spiralis (9, 15, 18, 20, 44).

(27) Cell with longitudinal furrow.

Protomastiginæ—

Colponema (7, 24, 25, 53).

Eugleninæ (34, 40)—

Cryptoglena (1, 14, 31, 37, 39).
Petalomonas (1, 24, 30, 41).
Anisonema (7, 24, 30, 41).

(28) Cell with longitudinal and transverse furrows.

Dinoflagellata—

Glenodinium (4, 13).

(29) Body sometimes amœboid or very metabolic.

Pantostomatinæ—

Cercomonas (7, 17, 22, 41, 48).
Cercobodo agilis (7, 18, 44).
„ *vibrans* (7, 13, 17, 46).
Helkesimastix (4, 14, 42).
Mastigamœba (1, 41).
Mastigella (1, 41).

Protomastiginæ—

Bodo, posterior end sometimes amœboid (7, 15, 16, 17, 22, 23, 24, 44, 45, 46, 49, 51, 53).
Heteromita (7, 14, 15, 24, 43, 48, 50).
Pleuromonas (7, 13, 16, 53).
Sainouron (3, 16, 43, 48).
[*Tetramitus rostratus*, not usually amœboid, but an amœboid phase has been described (10, 21, 22, 44).]

Chrysomonadinæ—

Oikomonas, posterior end sometimes amœboid (1, 13, 14, 15, 22, 48).
Chrysamœba (1, 14, 15, 31, 32, 36).
Polypseudopodius (2, 18, 49).

Eugleninæ (34, 40)—

Euglena, some species very metabolic (1, 20, 22, 30, 37, 39, 41).

SHAPE—*contd.*

(29) Body sometimes amœboid or very metabolic—*contd.*

Eugleninæ—*contd.*

Eutreptia, very metabolic (5, 18, 22, 34, 37, 39, 40).

Astasia (1, 41).

Distigma (7, 18, 41).

Peranema, very metabolic but with membrane having longitudinal striations (1, 17, 41).

Urceolus, very metabolic but with membrane having longitudinal striations (1, 17, 41).

Heteronema (7, 17).

(30) Body enclosed in a firm membrane or cuticle.

Protomastiginæ—

Allantion (3, 14, 16, 42).

Cryptomonadinæ (34)—

Chilomonas (6, 14, 34).

Cryptomonas (5, 14, 37).

Cyathomonas (5, 24, 34).

Rhodomonas (5, 15, 22, 38).

Eugleninæ (34, 40)—

Euglena, most species rather metabolic (1, 20, 22, 29, 37, 39, 41).

Phacus, membrane firm, usually with longitudinal striations (1, 22, 24, 37).

Clostenema (7, 18, 42).

Menoidium (1, 16, 19, 45).

Petalomonas (1, 24, 27, 41).

Scytomonas (1, 14, 41).

Anisonema (7, 24, 27, 41).

Entosiphon (7, 24).

Phytomonadinæ—

Chlamydomonas (5, 13, 37, 39, 45).

Polytoma (5, 14, 45, 46).

Parapolytoma (5, 14, 45).

Chlorogonium (5, 18, 22, 39).

Pandorina (5, 32, 37).

Chrysomonadinæ—

Mallomonas—cuticle covered with siliceous plates and bearing fine needle-like siliceous spines (1, 14, 40).

(31) Cell enclosed in a sheath, lorica, or test from which it can at times become free.

Protomastiginæ—

Salpingœca, sheath a thin lorica (1, 15, 33, 35).

Phalansterium, sheath thick and gelatinous (1, 13, 14, 15, 32, 35, 46, 52).

Spongomonas, sheath thick and gelatinous (5, 13, 24, 32, 45, 52).

Cladomonas, sheath thick and gelatinous (5, 13, 32, 52).

Chrysomonadinæ—

Chrysamœba, sheath thick and gelatinous (1, 14, 15, 29, 32, 36).

Eugleninæ (34, 40).

Trachelomonas, sheath a thin lorica (1, 13).

Cryptoglena ,, ,, (1, 14, 37, 39).

(32) Individual cells often united into colonies.

Protomastiginæ—

Codosiga, several cells attached to a common stalk (1, 14, 15, 33, 35, 47).

Phalansterium, gelatinous sheaths fused into an irregular mass (1, 13, 14, 15, 31, 35, 46, 52).

Spongomonas, gelatinous sheaths fused into an irregular mass (5, 13, 24, 31, 45, 52).

Cladomonas, many cells set in a branching gelatinous sheath (5, 13, 31, 52).

Chrysomonadinæ—

Cephalothamnium, several cells sometimes attached to a common stalk (2, 21, 22, 33).

Chrysamœba, cells set in gelatinous masses (1, 14, 15, 29, 31, 36).

Phytomonadinæ (30).

Pandorina, regular compact colonies—spherical or ellipsoidal (5, 30, 37).

(33) Cell with stalk.

Pantostomatinæ—

Actinomonas (1, 13, 36, 53).

(33) Cell with stalk—*contd.*

Protomastiginæ—

Codosiga, stalk long (1, 14, 15, 32, 35, 47).

Monosiga, stalk generally very short (1, 13, 14, 15, 35, 47).

Salpingœca, lorica stalked (1, 15, 31, 35).

Chrysomonadinæ—

Monas (*M. guttula*) (2, 13, 14, 39, 48).

Cephalothamnium (2, 21, 22, 32).

Physomonas (2, 14, 36).

(34) With permanent mouth and cytopharynx.

Cryptomonadinæ (30)—

Chilomonas (6, 14, 30).

Cryptomonas (5, 14, 30, 37).

Cyathomonas (5, 24, 30).

Rhodomonas, mouth small (5, 15, 22, 30, 38).

Eugleninæ (40)—A permanent cyto-pharyngeal opening is one of the characteristics of this order.

(35) Collar round base of flagellum.

Protomastiginæ—

Codosiga, collar large (1, 14, 15, 32, 33, 47).

Monosiga „ „ (1, 13, 14, 15, 33).

Salpingœca „ „ (1, 15, 31, 33).

Phalansterium, collar small (1, 13, 14, 15, 31, 32, 46, 52).

(36) Cell with fine radiating pseudopodia.

Pantostomatinæ—

Actinomonas (1, 13, 33, 53).

Chrysomonadinæ—

Physomonas (2, 13, 33).

Chrysamœba (1, 14, 15, 29, 31, 32).

(37) Cell containing chlorophyll.

Eugleninæ (34, 40)—

Euglena (1, 20, 22, 29, 30, 39, 41).

Eutreptia (5, 18, 22, 29, 34, 39, 40).

Phacus (1, 22, 24, 30).

Cryptoglena (1, 14, 31, 39).

Cryptomonadinæ (30, 34)—

Cryptomonas (5, 14).

(37) Cell containing chlorophyll—*contd.*
Phytomonadinæ (30)—
Chlamydomonas (5, 13, 30, 39, 45).
Pandorina (5, 32).

(38) Cell with red pigment.
Cryptomonadinæ (30, 34).
Rhodomonas (5, 15, 22, 30, 34).

(39) Stigma ("eye-spot") present.
Chrysomonadinæ—
Monas (*M. vivipara*—stigma absent from other species) (2, 13, 14, 33, 48).
Eugleninæ (34, 40)—
Euglena (most species) (1, 20, 22, 29, 30, 37, 41).
Eutreptia (5, 18, 22, 29, 37).
Cryptoglena (1, 14, 31, 37).
Phytomonadinæ (30).
Chlorogonium (5, 18, 22, 30).
Chlamydomonas (5, 13, 30, 37, 45).

(40) Complicated contractile vacuole system.
Chrysomonadinæ—
Mallomonas (1, 14, 30).
Eugleninæ: a complicated vacuole system is one of the features of this order (34).
Phytomonadinæ (30).
Allas (4, 14, 24, 42).

MOVEMENTS:—

(41) Creeping.
Pantostomatinæ—
Cercomonas (7, 17, 22, 29, 48).
Mastigamœba (1, 29).
Mastigella (1, 29).
Eugleninæ—
Astasia (1, 29).
Euglena (1, 20, 22, 29, 30, 37, 39)
Distigma (7, 18, 29).
Petalomonas (1, 24, 27, 30).
Scytomonas (1, 14, 30).
Peranema (1, 17, 29).
Urceolus (1, 17, 29).
Anisonema (7, 24, 27, 30)

MOVEMENTS—*contd.*

(42) Gliding.

Pantostomatinæ—
Helkesimastix (4, 14, 29).
Protomastiginæ—
Allantion (3, 14, 16, 30).
Phytomonadinæ (30)—
Allas (4, 14, 24, 40).
Eugleninæ (34, 40)—
Clostenema (7, 18, 30).

(43) Vibratory, with trailing flagellum clinging to the slide.

Protomastiginæ—
Heteromita globosa (7, 15, 29).
„ *repens* (7, 14, 29).
Sainouron (3, 16, 29, 48).

(44) Free-swimming: spiral.

Pantostomatinæ (29)—
Cercobodo agilis (7, 18, 29).
Protomastiginæ—
Bodo saltans (7, 16, 29, 53).
Spiromonas (7, 19, 26).
Tetramitus rostratus (10, 21, 22, 29).
„ *spiralis* (9, 15, 18, 20, 26).

(45) Free-swimming: rotating on axis but path not spiral.

Protomastiginæ—
Bodo celer (7, 15, 23, 29, 49).
Proleptomonas, rotation very rapid (1, 18, 46).
Spongomonas, movement appears flickering owing to the flattened shape (5, 13, 24, 31, 32, 52).
Eugleninæ (34, 40)—
Menoidium (1, 16, 19, 30).
Phytomonadinæ—
Chlamydomonas (5, 13, 30, 37, 39).
Polytoma (5, 14, 30, 46).
Parapolytoma (5, 14, 30).

(46) Free-swimming: vibratory, swimming forwards.

Pantostomatinæ—
Cercobodo vibrans (7, 13, 17, 29).

MOVEMENTS—*contd.*

(46) Free-swimming: vibratory, swimming forwards—*contd.*

Protomastiginæ—

Phalansterium, vibration very rapid (1, 13, 14, 15, 31, 32, 35, 52).

Bodo edax, progression very precipitate (7, 15, 23, 29).

Proleptomonas (1, 18, 45).

Phytomonadinæ (30)—

Polytoma, sometimes (5, 14, 30, 45).

(47) Free-swimming: swimming forwards slowly, with a vigorous longitudinal, piston-like vibration, or backwards in wide sweeps with a slight but rapid transverse vibration.

Protomastiginæ—

Monosiga (1, 13, 14, 15, 33, 35).

Codosiga (1, 14, 15, 32, 33, 35).

(48) Free-swimming: movements smooth, not spiral nor vibratory.

Pantostomatinæ—

Cercomonas, rarely: sinuous (7, 17, 22, 29, 41).

Protomastiginæ—

Heteromita obovata (7, 14, 29).

Sainouron, sinuous (3, 16, 29, 43).

Chrysomonadinæ—

Oikomonas, moves in wide curves but not spirals (1, 13, 14, 15, 22, 29).

Monas (2, 13, 14, 33, 39).

(49) Free-swimming: progress a series of erratic jerks.

Protomastiginæ—

Bodo caudatus, short, rapid jerks (7, 22, 24, 29).

„ *celer* (7, 15, 23, 29, 45).

Chrysomonadinæ—

Polypseudopodius, very active and erratic (2, 18, 29).

(50) Free-swimming: jerky, slow.

Protomastiginæ—

Heteromita ovata (7, 24, 29).

(51) Free-swimming: wriggling.

Protomastiginæ—

Bodo terricolus (7, 17, 29).

MOVEMENTS—*contd.*

(52) Sessile: vibratory.

Protomastiginæ—

Phalansterium (1, 13, 14, 15, 31, 32, 35, 46).

Spongomonas (5, 13, 24, 31, 32, 45).

Cladomonas (5, 13, 31, 32).

(53) Sessile: jerky.

Pantostomatinæ—

Actinomonas (1, 13, 33, 36).

Protomastiginæ—

Bodo saltans, tip of long flagellum attached to foreign body; organism motionless except for occasional very rapid jumps (7, 16, 29, 44).

Colponema (7, 24, 25, 27).

Pleuromonas (7, 13, 16, 29).

Rhizopoda.

ORDER I. AMŒBINA.—NAKED RHIZOPODS: PSEUDOPODIA OF VARIOUS FORMS WITHOUT ANY SUPPORTING STRUCTURES.

Family (i.) *Lobosa: pseudopodia blunt, pointed, or reduced to wave-like expansions of ectoplasm, but never filamentous nor reticulate.*

A satisfactory classification of the amœbæ still remains to be found. The grouping adopted in the following pages is a purely artificial one, aiming solely at facilitating identification.

(i.) *Limax group.*—Small amœbæ typically with a single rounded pseudopodium by means of which they crawl along, but sometimes several finger-like pseudopodia are formed simultaneously. Nucleus with a well-defined karyosome. This group includes most of the common soil amœbæ. They feed exclusively on bacteria, and from this point of view are the most important of all the soil protozoa.

Their feeding habits have already been briefly discussed (see above, p. 2).

This group falls into three sub-groups :—

(a) *Nægleria sub-group.*—Active forms having a flagellate stage, and with large polar caps in the dividing nucleus.

Nægleria gruberi (Schardinger) Wilson.—Amœboid form a typical limax, length 10 to 20 μ, though much smaller forms are sometimes found ; nucleus generally clearly visible near the centre, and contractile vacuole near the hind end (Plate V., Fig. 3). Flagellate form much less commonly seen (it can often be produced by pouring pure water on to a culture of the amœbæ) ; ovoid to pyriform with two equal flagella slightly longer than the body arising at the anterior end, both directed forwards ; nucleus near the base of the flagella ; contractile vacuole posterior (Plate V., Fig. 4). Cysts spherical, diameter 7 to 14 μ, with a thin, smooth outer wall and a thicker inner wall pierced by 3 to 8 openings to which the protoplasmic contents are attached, hence the name *Amœba punctata*, Dangeard, which is sometimes applied to it. The nucleus is visible as a large clear space in the middle of the cyst ; generally only 1 nucleus is present, but occasionally cysts with 2, 4, or 8 nuclei are found (Plate I., Fig. 21).

This species has many synonyms, viz., the generic names *Amœba*, *Dimastigamœba*, *Vahlkampfia*, *Wasielewskia*, and the specific names *punctata*, and ? *diplomitotica* : *Amœba tachypodia*, Gläser [47] and *Vahlkampfia soli*, Martin and Lewin.[78]

This is one of the most characteristic of soil protozoa, and has been mentioned by practically every investigator.

N. bistadialis (Pusch.).—Very similar to *N. gruberi*, but in the flagellate stage one of the flagella is short (not more than half the body length) and is directed backwards. The cysts are spherical, and the inner wall not perforated. In the older cysts the protoplasmic contents shrink considerably from the wall, and the space between becomes filled with disorganised debris. This is one of the species obtained by Puschkarew from the air which Martin and Lewin claim to have found in soils. It has not been recorded by any other soil investigators, but Wasielewski and Kühn,[118] who described it in detail, obtained it from straw.

(b) *Hartmanella sub-group.*—Limax amœbæ without any flagellate stage, and with no polar caps in the dividing nucleus.

Hartmanella hyalina (Dangeard) Alex.—Active form very like *N. gruberi*, but usually slightly larger: protoplasm rather more fluid and pseudopodia generally formed "eruptively," *i.e.*, they burst suddenly through the surface of the amœba and the granular protoplasm flows rapidly into the newly-formed process; generally, instead of at once forming a long finger-like pseudopodium the eruption flows round the outside of the original surface of the body which ultimately becomes absorbed. The cysts (Plate I., Fig. 20) are spherical; outer wall usually more or less crinkled; walls not perforated; protoplasmic

contents rounded lying quite freely within the wall; nucleus not so visible as in *N. gruberi*.

This species is, if anything, even more widely spread in soils than *N. gruberi*, though much less frequently recorded, probably owing to confusion with the latter species. As mentioned above (p. 59), the two species are not often found together in the same soil.

Amœba lawesiana, Goodey,[52] found in an old stored Rothamsted soil, is probably identical with the last species. It appears to differ only in having a compact equatorial ring of granules in the dividing nucleus instead of small spherical chromosomes, and in having a connecting strand in the telophase of the nuclear division which is absent in *H. hyalina*.

A. agricola, Goodey.[52]—This species was obtained from another old Rothamsted soil by Goodey, who gives very little information about its appearance in the living condition. It is of an irregular limax shape, length 12 to 15 μ, without any clear distinction between the ecto- and endo-plasms: contractile vacuoles and cysts are not mentioned. Division takes place while the animal is still in an irregular form. The nucleus has no peripheral chromatin, and in dividing has no true spindle and no proper equatorial plate.

A. horticola, Nägler.[53]—A rapidly-moving limax amœba with large pseudopodia; length 15 to 25 μ; ecto- and endo-plasms clearly distinguishable, the latter being coarsely granular and showing strong streaming movements; contractile vacuole single and

not easily seen; nucleus easily visible in the unstained living organism, in division it has six chromosomes; cysts, diameter 10 μ, spherical to ellipsoidal, with nucleus very much reduced and almost invisible; from Nägler's figures there appears to be a thin flexible and rather irregular outer wall raised some distance from the thicker imperforate inner wall which is almost completely filled by the protoplasmic contents.

Found by Nägler in garden soil.

(c) *Guttula sub-group.*—Limax amœbæ without a flagellate stage, but with a large polar mass in the dividing nucleus.

Amœba (*Hyalodiscus*) *guttula*, Duj.—A broader and more ovoid form than the other limax amœbæ, the anterior pseudopodium being a broad expansion of the ectoplasm rather than a finger-like process; very transparent; size 30 to 35 μ × 20 to 25 μ (Cash[17]).

This has been recorded by a number of soil investigators. Wolff[120] (characteristic of arable soils), Francé[44] (widely distributed in meadows, flower-pots, etc., but not in woods or in arable fields), Fellers and Allison[30] (occasional); Fantham and Taylor and Fantham and Paterson;[35, 87] Yakimoff and Zérèn[126] (in 12 out of 15 soils).

As the identification of the limax amœbæ is based mainly on the presence or absence of a flagellate stage and on cytological characteristics, except when one is dealing with characteristic forms such as *N. gruberi* and *H. hyalina*, identification is generally impossible except in more or less pure cultures.

Naturally, therefore, many forms occur which cannot be identified, and nearly all records in consequence contain frequent references to "*Amœba limax.*" Such unidentified forms appeared in cultures of 56 of our soils. One form which appears fairly frequently is that referred to in previous papers[26, 100, 101] as Sp. *a*. Unfortunately attempts to isolate pure cultures have failed and consequently nothing can be added to the following preliminary description published in 1922.[26] "A very small limax amœba. . . . Even when fully extended it rarely exceeds 10μ in length. Its movements are slow and it is never observed to travel far in any one direction. More frequently short, knobby pseudopodia are formed first at one point and then at another, and withdrawn again without any progression having been effected. In the living animal the protoplasm is refractile, and does not appear to be vacuolated or to show any structure, while the nucleus is not visible and no contractile vacuole has been observed. Staining reveals a nucleus composed of a karyosome and a very thin nuclear membrane, with no peripheral chromatin. Nuclear division is promitotic, resembling that described for *A. froschi.*" It was observed in about 13 of the soils examined here. Allison found it in 95 per cent. of the American soils examined, and Perey found amœbæ closely resembling it in 3 out of 5 French soils.

A. nitrophila, Beijerinck.[8]—This interesting limax amœba was found by Beijerinck in large numbers in an agar culture of nitrifying organisms. In the active

condition its size (? length) is 15 to 20 μ; it has very clear protoplasm, a nucleus which is easily visible, and generally two vacuoles, of which one is contractile and the other not. The contractile vacuole is often surrounded by three small accessory vacuoles. The cysts (diameter 10 to 11 μ) have a thick and irregular outer wall which disappears before excystation, leaving the smooth spherical inner wall, which splits open. The formation of the cysts is peculiar in that it is endogenous, and the whole of the protoplasm is not utilised. From Beijerinck's diagrams the newly-excysted amœbæ are of the typical limax type, but the older ones are less regular in shape. No cytological details are given, so it is impossible to say to which of the sub-groups it belongs.

(ii.) *Verrucosa group.* — Amœbæ with an ectoplasmal pellicle; pseudopodia in the form of ridges or folds of ectoplasm. Nucleus large, containing one or many blocks of chromatin.

Amœba verrucosa, Ehrbg. — A large amœba, generally about 120 μ in diameter, though the ones found in soil cultures are often very much smaller (20 to 50 μ); shape roughly spherical; endoplasm granular, ectoplasm clear and corrugated; nucleus ellipsoidal, and in large individuals about 35 × 18 μ in size, consisting of a thick membrane under which is a layer of chromatin masses; contractile vacuole single and often reaching a very considerable size (diameter 50 μ) before contracting.

Amœba terricola, Greef, is most probably a synonym for this species. Yonge[127] quotes Rhumbler

as having demonstrated the digestion of cellulose by this amœba. It has been found in soils from Spitsbergen, Greenland, Cape Verde Island, Mauritius, Argentine, and India (Pusa), and has also been recorded by Wolff (a "Leitform" in arable soils), Goodey, Francé (in woodlands but not in meadows), Nowikoff, Fantham and Taylor, Fantham and Paterson (in many South African soils, both water-logged and not water-logged), and Yakimoff and Zérèn (in 13 out of 15 soils).

A. (*Sappinia*) *diploidea*, Hartmann and Nägler.—In its typical form this is very like a small specimen of *A. verrucosa*, but can be distinguished by the presence of two nuclei which are usually easily visible and which lie close together. The ridging of the stiff ectoplasm is more marked than in *A. verrucosa*, and the surface is often thrown into strong folds and irregular processes, but at times the protoplasm becomes more fluid and the amœba may even approach the appearance of a large limax form. The two nuclei lying closely side by side are, however, always characteristic (Plate V., Fig. 2). Diameter about 15 to 30 μ. Conjugation occurs in thin-walled spherical cysts.

This is a common and characteristic soil species and was found in soils from Egypt, Palestine, West Indies, Cape Verde Island, Spitsbergen, and Japan, as well as frequently in Rothamsted soils. Martin[76] found it in sick soils, and Craig and Calkins both record it as a form which can be obtained from garden soil.

A. striata, Penard.—A very clear, glassy amœba with finely granulated endoplasm surrounded by a border of clear ectoplasm, and a very fine pellicle. Shape when progressing oval, about a half to two-thirds as broad as long; length 30 to 60 μ, nucleus visible near middle of amœba consisting of a spherical karyosome (diameter about 4 to 5 μ) surrounded by a narrow clear zone; contractile vacuole single, formed by the coalescence of several small ones. Penard says that there are two contractile vacuoles but only one has been observed in the soil forms. Progression steady and fairly rapid, the ectoplasmic border being wider at the front end than elsewhere, and the endoplasmic streaming being easily visible; during progression the pellicle is generally thrown into three or four longitudinal ridges, and when movement stops the outline often becomes sinuous.

Found in 2 soils from Mauritius and Greenland, and also recorded by Francé.

Greef[54] described other amœbæ of this type (*A. alba*, *A. sphæronucleolus*, and *A. fibrillosa*) and called them all "soil amœbæ," but as his material was obtained from mosses and the species in question have not been otherwise recorded from soils, they are no doubt moss dwellers rather than soil dwellers.

(iii.) *Lamellipodia group.*—Forms similar to the preceding group but with the pellicle less strongly developed; pseudopodia broad sheets of ectoplasm.

Amœba glebæ, Dobell.[30]—Diameter when rounded 12 to 20 μ; endo- and ecto-plasms clearly differentiated, the former vacuolar and full of refringent granules,

the latter well-developed, and hyaline sometimes forming a border all round; pseudopodia pointed and with the ectoplasm often drawn out into thin, web-like sheets between them; contractile vacuole single. Cysts spherical, diameter 10 to 13 μ, with thick, smooth outer wall without pores which renders the contents difficult to stain; protoplasmic contents filled with refringent granules.

The nucleus is very characteristic, consisting of a large karyosome composed of chromatin grains set in a matrix of plastin surrounded by a clear zone crossed by fine strands on which are set a single ring of palely-staining granules. This species differs from *A. lamellipodia*, Gläser, which has not been found in soil, only in being slightly smaller and in having one instead of several contractile vacuoles. It was first obtained by Dobell from soil, and forms very like it have been found in soils from Kenia, Sudan, Egypt, Palestine, Grenada, and Rothamsted, though their actual identity was uncertain, except in the case of the English soil.

Amœba actinophora, Auerbach. — Flattened and disc-shaped; about 25 to 40 μ long; when active always with a wide border of very transparent ectoplasm entirely surrounding it, except during the extrusion of fæcal matter when the endoplasm extends to the periphery at the point of extrusion; when the amœba is not active, however, the ectoplasm ceases to be distinguishable; long, fine-pointed pseudopodia arise from the endoplasm, and extend into the ectoplasm, sometimes penetrating far beyond it; changes

of shape are rapid but progression slow; contractile vacuoles one to three, generally anterior, and sometimes formed by the coalescence of two smaller ones. The cyst and mode of division have not been observed, but Martin and Lewin have described an *Amœba cucumis* from a cucumber soil which resembles this species very closely, except that a contractile vacuole was not found. They described a thin-walled spherical cyst and a process of nuclear division in which the karyosome becomes broken up into granules, arranged in a large equatorial plate which ultimately doubles, but without the formation of a spindle. Whether these two species are identical remains uncertain, as do also their relations with *A. glebæ*, Dobell, and *A. lamellipodia*, Gläser. The preceding description was made from organisms found in one Spitsbergen and in two Argentine soils.

A. gobanniensis, Martin and Lewin.—This amœba was found by Martin and Lewin[78] in a seedling bed, and was regarded by them as being very closely allied to their *A. cucumis* and to *A. lamellipodia*, Gläser, differing mainly in the absence of the long-pointed pseudopodia. "In life this amœba is a very sluggish form, and is readily recognised by the extraordinary development of its ectoplasm; . . . the resting form is characterised by a large plate-like ectoplasmic pseudopodium surrounding the animal. In movement a long axial pseudopodium from the entoplasmic core seems to be thrown out by the animal." This amœba seems also very similar to *Amœba striata*, Penard, described above.

A. velata, Parona.—A small amœba (dimensions

not given) with endoplasm full of small granules and food bodies ; nucleus small and spherical, and often invisible ; two to five contractile vacuoles. It progresses by means of a broad, wave-like sheet of ectoplasm and closely resembles a colourless *Hyalodiscus*, but the characteristic feature is the formation of a long, temporary tentacle-like pseudopodium. This, or an allied form, was found by Francé[44] in a flower-pot at Munich.

(iv.) *Proteus group.*—Very big amœbæ, of very changeable shape, sometimes rather like a big "limax," clavate, palmate, or with numerous long cylindrical pseudopodia ; protoplasm containing numerous crystalline bodies ; nucleus (occasionally double) large and containing many chromatinic masses ; contractile vacuole usually single. The feeding habits of these amœbæ have been the subject of a series of valuable studies by Schaeffer,[102] who has demonstrated that they possess very considerable powers of discrimination and that the choice of food may be modified by circumstances. In general it is moving objects which are most readily ingested, and it seems probable that in the soil their food consists mainly of algæ. Schaeffer[102] has also divided this group into three species, *A. proteus*, *A. discoides*, and *A. dubia*. All of them are considerably larger than the form found in soil cultures, which is generally only about 60 to 120 μ long, whereas the species described by Schaeffer vary from 400 to 1200 μ. Cash gives the size of *A. proteus* as 200 μ when rounded and 400 to 450 μ when extended.

This form was found in 12 soils from England, Greenland, Mauritius, Tristan da Cunha (?), Gough Island, Argentine, Sudan, India, and Ocean Island (?).

It has also been recorded by Ross and Thomson (in Egyptian sand), Fellers and Allison (occasional, length 70 to 250 μ), Francé (in meadows but not in arable or woodland soils), Fantham and Taylor, and Fantham and Paterson (in South African soils of all types).

Unclassified Amœbæ. *A. albida*, Nägler.—A non-pelliculate amœba, diameter when rounded about 20 to 30 μ; very hyaline and transparent, with large flattened ectoplasmic pseudopodia, rounded at the ends; one (occasionally two) contractile vacuole; nucleus large and easily visible in life, consisting of a karyosome (generally containing one to three vacuoles), relatively wide *Kernsaftzone*, and a membrane under which is a plentiful layer of chromatin grains. The cysts are spherical, diameter 15 μ, occasionally 20 to 25 μ; in the larger ones the contents are rather shrunken and present a polyhedral appearance (Plate I., Fig. 22). Nuclear division by promitosis; autogamy in cysts.

This species was found by Nägler in garden soil and very similar forms have been found in a number of other soils, the only apparent difference being that, in addition to the broad, thin, sheet-like ectoplasmal pseudopodia, long fine pseudopodia are often found which sometimes branch and are sometimes pointed at the tips. The spherical cysts with polyhedral contents are very characteristic. Like Nägler's form

this amœbæ is infested with parasites. It has been found in soils from Mauritius (4 soils), Argentine, Greenland, and Ocean Island.

A. polyphaga, Pusch.—Found in rain-water and recorded from soil by Martin and Lewin; is probably identical with the foregoing species.

Amœba radiosa, Ehrbg.—Amœbæ of the *radiosa* form (*i.e.*, possessing straight, tapering pseudopodia which radiate in all directions) are frequently found in soils. A number of different species are, however, capable of assuming this appearance, and consequently without prolonged observation it is impossible to assign these forms to any definite species.

Pelomyxa palustris, Greef.—The largest of the amœboid rhizopods; diameter from 150 μ up to 2 mm; shape rounded or lobed, body opaque and full of foreign matter; nuclei small and very numerous.

Fantham and Paterson[38] in soils from the Cape coastal belt, but not from other parts of South Africa.

Family (ii.) *Reticulosa.—Pseudopodia long and anastomosing, often filamentous and reticulate.*

Biomyxa vagans, Leidy.—Shape and size exceedingly variable, sometimes extending to several hundred microns; protoplasm finely granular, semi-fluid and colourless; pseudopodia long, branching filaments which often anastomose, forming a net-work; numerous small contractile vacuoles; nucleus single and visible in the living unstained animal (in this it differs from *Arachnula impatiens*, Cienk., which has many obscure nuclei). (Plate V., Fig. 1.)

Found in a few soils from Palestine, Sudan, West Indies, and Elephant Island, but possibly rather more common than these records indicate, as it is easily overlooked even in cultures in which it is fairly numerous.

Gephyramœba delicatula, Goodey.[50] — Protoplast stretched out in a thin sheet or forming long cylindrical branching arms 3 to 4 μ across, with rounded, and sometimes swollen, ends (not filamentous as in *Biomyxa*) which often coalesce with one another. Numerous minute contractile vacuoles. Nucleus single, large, and often very distorted by the movements of the arms. Protoplasm clear, not refractile, and finely granular. Length when fully extended, 60 μ to 250 μ. Cyst spherical with a single, rather thin, smooth wall without any pores or markings; contents transparent and finely vacuolated with nucleus faintly visible.

Found by Goodey in a culture from a soil receiving large quantities of farmyard manure. Also in a virgin pasture soil from Canada (sample 85). Cultures of this organism have been obtained from both ordinary dung manure and from "synthetic" straw manure.

Leptomyxa, Goodey.[50] — A form something like *Gephyramœba* but with pseudopodia often filose, many minute nuclei; double-walled cysts. Goodey found two species in heavily dunged soils—*L. reticulata*, in which the branches anastomose and the ectocysts often contain more than one endocyst; and *L. flabellata*, in which the pseudopodia do not anastomose and the ectocysts (which have well-defined prominences) never

contain more than one endocyst. Yakimoff and Zérèn found a proteomyxan which was possibly *L. reticulata* in a market garden soil.

Family (iii.) *Pseudo-Heliozoa. — More or less spherical forms; shape somewhat variable and protoplasm not vacuolated as in the Heliozoa and not differentiated into ecto- and endo-plasms; pseudopodia straight, fine, and pointed, sometimes branched and radiating on all sides of the body.*

Nuclearia sp. (Plate IV., Figs. 10, 11).—The form found in the soil is usually spherical in shape, though when moving it may become broadly spindle-shaped or triangular; diameter 9 to 15 μ; protoplasm coarsely granular or lumpy so that the nucleus (which is single) is obscured in the living, unstained animal; rays straight, fine, and tapering, slightly motile, and a little longer than the diameter of the organism. Bacteria, etc., are never seen lying within the zone of the rays, which are in fact so fine that this clear zone is generally the most obvious indication of their presence; but with good optical apparatus some twelve to twenty rays can be observed crossing it. The very clear mucilaginous envelope found in some species of *Nuclearia* is, however, entirely absent. Contractile vacuole single, formed by the coalescence of two or three smaller ones, attains a diameter of about 4 μ before contracting. The organism usually appears motionless, but at times can move fairly actively. The movement is effected by certain of the rays adhering by their tips to the microscope

slide and then by their tension drawing the rest of the organism after them. Sometimes two or three groups of rays at different points on the body become attached simultaneously, causing the body to become drawn out to an elongated or triangular shape until one of the groups of rays detaches itself from the slide; the organism is then drawn along by those which remain attached, resuming at the same time its spherical shape. Often this takes place with a sudden jerk, indicating that the animal possesses considerable elasticity and had been subjected to considerable tension by the pull of the rays; but this pull is not produced simply by their contraction, since they are decidedly longer instead of shorter than the rays on the other parts of the body which are not producing any tension. No pseudopodia other than these fine rays are produced, either in locomotion or in feeding, which seems to take place by the food body (generally a coccus) moving slowly down the rays (presumably by some streaming motion of the surface of the ray) to the surface of the organism into which it seems to sink. Division occurs in the active condition; the daughter organisms remaining connected for some time like a dumb-bell, by a narrow stalk. This species seems to agree entirely with the descriptions of *N. simplex*, Cienk., except in its smaller size and in the fact that the latter encysts readily in cultures whereas the present form usually fails altogether to encyst. In the course of the series of daily counts of protozoa carried out at Rothamsted it was found to be almost invariably present, often to the

number of several hundreds or even thousands per gramme of soil. It was found in 37 of the 148 soils examined here, and *N. simplex* has been recorded by Wolff (field soils), Perey (in 4 out of 5 French soils), Allison (in 40 per cent. of his U.S.A. soils), and Fantham and Paterson (in soils from the Cape coastal belt, but not from other parts of South Africa).

Vampyrella laterita (Fresen.) Leidy. — Usually spherical, with straight radiating pseudopodia, diameter 30 to 40 μ, like a *Nuclearia*, but reddish in colour owing to feeding on chlorophyll-containing algæ. In addition to the long fine rays, wave-like, lobate or digitate processes of clear ectoplasm are formed at the periphery. There is no nucleus, but scattered grains of nuclear substance are found.

Fellers and Allison (in one locality only).

Monobia confluens, Schneider.—A somewhat similar form in which, however, colonies of a considerable number of individuals are formed by the fusion of their pseudopodia.

Wolff (once only).

ORDER 2.—HELIOZOA. SPHERICAL FORMS WITH FINE RADIATING PSEUDOPODIA EACH USUALLY CONTAINING A STIFF AXIAL ROD: ENDOPLASM SURROUNDED BY A VACUOLATED ZONE OF ECTOPLASM.

Sub-order (i.) *Aphrothoraca.—Heliozoa without any envelope or investment except during encystment.*

Actinophrys, Ehrbg.—Nucleus single; endoplasm colourless and granular, ectoplasm full of large vacuoles; diameter 40 to 50 μ.

Greenland, India (Coimbatore). Individuals of this genus were also found in soils from St Kitts and Spitsbergen.

Actinophrys sol, Ehrbg., has also been recorded by Fellers and Allison (diameter 50 to 100 μ, occasional), Yakimoff and Zérèn (rare, found only in two market garden soils), Fantham and Taylor and Fantham and Paterson (fairly widely distributed).

Actinosphærium, Stein.—Resembling *Actinophrys*, but having more than one nucleus. A single record of this genus is given by Taylor and Burns from the irrigated soils of the Nile delta.

Sub-order (ii.) *Chalarothoraca. — Heliozoa with an envelope containing solid structures.*

Raphidiophrys, Archer. — Protoplasmal envelope containing siliceous spicules (these are sometimes not easily visible).

Fellers and Allison (rare).

Acanthocystis aculeata, Hertwig and Lesser.—Envelope composed of siliceous scales, and stout, pointed radial spines, diameter 35 to 40 μ.

Fantham and Taylor (in an uncultivated soil from Orange Free State). Fantham and Paterson (in soils from the Karroo and from the coastal zone).

Sub-order (iii.) *Desmothoraca.—Heliozoa with a continuous perforated envelope; often stalked.*

Clathrulina elegans, Cienk.—Envelope spherical, diameter 60 to 90 μ (Leidy 30 to 44 μ) with large circular or polygonal openings; length of stalk two to four times diameter of envelope.

Fellers and Allison (rare).

ORDER 3. — TESTACEA. RHIZOPODS PROVIDED WITH A SINGLE-CHAMBERED TEST INTO WHICH THE WHOLE BODY CAN BE COMPLETELY WITHDRAWN.

The morphology of the tests makes these organisms easier to identify than those in any other groups of protozoa, and the classification contains fewer ambiguities. That followed here is taken from Cash and Wailes' monograph,[17] from which also the descriptive notes are mostly adapted. Most of the forms which have been recorded from the soil are common on mosses, and it is very probable that many of the following records refer simply to empty tests found in soil on which mosses were growing, and that the organisms to which they belonged were never actually living in the soil. There is little doubt, however, that some species do lead an active life in soils, particularly in those containing abundant organic matter.

Family (i.) *Arcellida.—Test chitinous and homogeneous, with or without extraneous matter adhering; pseudopodia generally digitate, rarely lobed.*

Arcella, Ehrbg. — Test membranous, generally brown or yellow in colour, circular in dorsal view, and hemispherical or plano-convex in side view; mouth circular, central, and forming an inverted funnel.

This genus was found in large numbers in peat by Müller.[81] Francé states that it is found in forest soils and in wet humus soils, but not in soils that are dry or deficient in humus.

A. vulgaris, Ehrbg.—Test a hemispherical dome, diameter about 70 μ. Found in a single soil from Prince Edward Island. Also recorded by Goodey

(sewage soil), Wolff (a "Leitform" in field soils), Francé (in damp soils and woodland soils, but not in meadows or arable fields); Fellers and Allison (rare), Nowikoff, Fantham and Taylor, and Fantham and Paterson (in one soil each).

A. discoides, Ehrbg.—A very similar form, but more transparent and less convex in side view, the height being only $\frac{1}{4}$ to $\frac{1}{3}$ the diameter. Two (? 3) South Georgian soils. Wolff records another form, possibly *A. dentata*, Ehrbg.

Pseudochlamys patella, Claparède and Lachmann. —Test simple and discoid like an inverted saucer; colourless, very flexible, and often rolled up like a scroll when young, but becoming more rigid and brown in colour later on; diameter 40 to 45 μ.

Found by Francé in meadows, woods, arable fields, under moss and in flower-pots, but never numerous.

Corycia flava (Greef) Penard.—In young stages very similar to *P. patella*, but when older the flexible membrane becomes yellowish-brown in colour, usually having some adhering foreign particles, and there is a very fine membrane on the under surface which sometimes completely closes the test. Diameter when adult 80 to 100 μ; two nuclei. Francé.

Parmulina obtecta (Gruber) Penard. — Test yellowish, chitinous and rather mucilaginous, generally covered with foreign bodies, shape hemispherical in side view, oral surface oval, but capable of being closed, the aperture being then reduced to a long narrow slit; animal amœboid. Size very variable; average diameter about 30 μ. Francé.

Centropyxis aculeata (Ehrbg.) Stein.—Test chitinous and opaque, more or less covered with sand particles, etc., circular in dorsal view, in side view depressed and shallower at one side than the other; mouth eccentric, situated at the shallower side, and rather irregular in shape. Generally the test of this species has a variable number of spines, but the form found in the soil is always Leidy's var. *ecornis* which differs from the typical members of the species also in being rather smaller. Diameter 100 to 135 μ. Found in two South Georgian soils and in one from the Congo.

C. lævigata, Penard.—Test more dome-shaped than that of *C. aculeata*, and mouth obliquely invaginated, terminating in an inverted neck; diameter about 100 μ (Plate V., Figs. 6, 7).

Found in soils from South Georgia (2), Spitsbergen (2), Greenland (2, ? 3) and Canada (Prince Edward Island). *Centropyxis* (species not identified) was also found in three soils from Gough Island, and have been recorded by Nowikoff.

Difflugia, Leclerc.—Tests in some cases very similar to those of *Centropyxis*, but differing generally in shape, the height being greater than the diameter, *i.e.*, they are globular, elongated or pyriform, etc., with a terminal mouth; transverse section generally circular.

Müller[81] found species of *Difflugia* in great numbers in peat, and according to Francé[44] they are the characteristic forms of woodland soils, but occur also in meadows. The latter investigator had previously found them in both wet and very dry soils.[43]

D. oblonga, Ehrbg. (= *D. pyriformis*, Perty).—A variable form, typically oblong or pear-shaped, tapering towards the mouth, which is quite terminal. Size also very variable, 100 to 300 μ long × 50 to 100 μ broad.

South Georgia and Mauritius (in one soil only from each): also recorded by Fellers and Allison (rare, found in one locality only, length 40 to 200 μ), Francé (meadow and arable soils, but not in woodlands), and Fantham and Taylor and Fantham and Paterson.

D. penardi, Wailes (= *D. fallax*, Penard).—Somewhat like *D. oblonga*, but rather shorter and broader; test not forming a neck; rather transparent. Size 60 to 85 μ × 30 μ.

Found in a single Spitsbergen soil.

D. lucida, Penard.—Test very transparent, thin, chitinous, and covered with transparent irregular siliceous scales, of which those around the mouth are arranged more regularly than the others. Very compressed; in narrow view the sides are nearly parallel, but in broad view the aboral end is domed and the sides taper towards the mouth. Length 60 to 80 μ, greatest width about 50 μ. Francé.

D. globula (Ehrbg.) (= *D. globulosa*, Duj.).—Test globular with a circular mouth not invaginated. Diameter 15 to 50 μ. The empty tests are indistinguishable from those of *Phygauella*, in the living forms of which, however, the pseudopodia are pointed instead of being blunt as in the present species.

This is a fairly common species, having been

found in 16 soils from Spitsbergen, Greenland, Canada, Argentine, Azores, Congo, Mauritius, Ocean Island, and South Georgia. Also recorded by Goodey[49] (sewage soil), Fellers and Allison (rare), Francé (in woodland, meadow, and arable soils), Fantham and Taylor and Fantham and Paterson (in many different types of soils).

D. urceolata, Carter.—A large, ovoid, rotund test constricted to form a short neck and then expanded into a rim round the mouth. Length 220 to 230 μ, breadth 150 to 200 μ.

Francé (woods, meadows, and arable soils).

D. lobostoma, Leidy.—Test sub-spherical to ovoid without a neck, covered with fine sand-grains, etc., opaque. Border of mouth with 3 to 6 regular lobes. Diameter 80 to 115 μ.

Found in a sandy orange soil from Palestine, and by Francé under moss.

D. arcula, Leidy. — Test hemispherical, base slightly concave but not invaginated; mouth triangular, irregularly trilobed, or roughly quadrangular; diameter of base about 90 μ.

Tristan da Cunha; (?) Canada (Ottawa and Brandon). Found by Francé under moss.

D. constricta (Ehrbg.) Leidy.—An exceedingly variable form (length 80 to 120 μ) characterised by an excentric antero-inferior mouth, the edges of which are often more or less inverted. Tests of this species often have two or more spines, but the forms found in the soil are always spineless (Plate V., Figs. 8, 9). Individuals are often found which resemble *Centropyxis*

aculeata very closely, but generally *D. constricta* is smaller. Fairly common in soils, and found in 25 from Spitsbergen, Greenland, South Georgia, Gough Island, Canada, Argentine, and Ocean Island. Like many of the other testaceous rhizopods it seems particularly characteristic of Arctic soils. Also recorded by Wolff in field soils, and Francé in woodland and meadow soils but not in arable fields.

D. craterella, Francé.—Shape of test like that of *Arcella discoides*, mouth irregular in outline and strongly invaginated; test encrusted with siliceous platelets; colour brown. Diameter 42 μ, height 23 μ, diameter of the mouth 12 μ. It differs from *Centropyxis lævigata* in being smaller and more flattened and in having the mouth more deeply invaginated and more irregular.

Francé (wood and meadow soils but not arable fields).

Phryganella acropodia (Hertwig and Lesser) (= *P. hemispherica*, Penard). Very like *Difflugia globula* but pseudopodia pointed at the tips instead of rounded. Diameter 30 to 50 μ. As the majority of tests found in soils are usually empty it is generally impossible to distinguish between these two forms. Francé.

P. nidula, Penard.—A much larger form (diameter 180 to 190 μ) heavily encrusted with sand grains, etc.

Found by Francé once only in an Alpine meadow, and stated by him to be found in meadows but not in woods or arable fields.

Difflugiella sp., Cash. — Test a thin, flexible chitinous structure, ovoid and not compressed; size

40 × 28 μ; two characteristic types of pseudopodia, "one lobular or digitate, protruding centrally from the mouth of the test, and terminated by a short apiculus, the other longer, straight, thin, tapering to a point, and projected laterally from each side."[17]

Francé[44] in arable and meadow soils, not in woodlands.

A very small organism closely resembling this in many respects has been found in a number of soils from Argentine, Canada, Greenland, Serbia, Australia, Congo, and India. The test, as in *Difflugiella*, is thin, transparent, somewhat flexible and apparently quite structureless; it is ovoid (narrower at the oral than at the aboral end), and circular in section. The nucleus is visible at the aboral end, surrounded by a clear zone much as in *Lecythium*, and there is a contractile vacuole near the middle. The protoplasm is clear except the central zone which usually contains large granules. The test is considerably thicker than that of *Lecythium*, from which also and from *Difflugiella* it differs in the nature of the pseudopodium. The only type of pseudopodia that has been observed is a simple rounded knob or disc of clear protoplasm protruding from the aperture of the test. A similar pseudopodium is found in *Leptochlamys*, but in this genus the nucleus is of a different type and the shape and dimensions of the test are also different (see also under *Pseudodifflugia*).

Hyalosphenia, Stein.—Test homogeneous, hyaline, ovoid to pyriform, and generally compressed laterally; surface either plain or pitted with depressions of various shapes according to the species; plasma only partially filling the test and attached to it by threads of ectoplasm. Three to five simple, digitate, blunt pseudopodia.

H. minuta, Cash.—A strongly compressed form, with mouth forming a notch when seen in side view. Size 35 to 40 μ × 20 to 25 μ.

Spitsbergen (1 soil only).

H. elegans, Leidy.—A larger form (75 to 100 μ × 60 μ), flask-shaped with a distinct neck; surface of test covered with hemispherical pits.

Francé (garden soil at an elevation of 1550 m.).

Francé also records the presence in soils of *H. cuneata*, Stein, *H. papilio*, Leidy, and *H. tincta*, Leidy, all typically moss forms.

Nebela, Leidy. — Tests thin and transparent, covered with circular, oval, or rectangular discs or plates irregularly arranged, ovate to pyriform and generally compressed.

N. collaris (Ehrbg.) Leidy.—Test pyriform, often with a slight neck in broad view, oblong and without a notch at the mouth in side view (Plate V., Fig. 13). Length about 130 μ.

South Georgia, ? Gough Island, Greenland, ? Japan. Francé (not uncommon in meadows, woods, and moors, but absent from arable soil and from dry poor soils).

N. lageniformis, Penard. — Characterised by possessing a neck which is somewhat swollen at the middle and is about $\frac{1}{3}$ the total length of the test. Size about 120 μ × 65 μ.

Spitsbergen (1 soil only). Francé (under moss). Other species mentioned by Francé are *N. flabellula*, Leidy, and *N. bigibbosa*, Penard.

Quadrula, Schulze.—Thin, chitinous test covered with transparent quadrangular plates arranged in rows and rarely overlapping.

Q. symmetrica (Wallich) Schulze. Test pyriform, narrowing towards the mouth, compressed laterally,

plates arranged in obliquely transverse rows and generally smaller near the mouth. Size variable; about 96 $\mu \times 60$ to 70 μ on the average. Francé.

Q. irregularis, Archer. — A small species: in broad view nearly circular without a neck, oval and slightly notched at the mouth in side view; mouth elliptic or reduced to a narrow slit; plates generally very uniform and set in regular oblique rows (Plate V., Fig. 14). Diameter 30 to 38 μ.

Spitsbergen, Mauritius, Ocean Island (2 soils). Francé found *Q. globulosa*, Penard (which appears to be identical with this species), once in a decomposing humus.

Heleopera, Leidy.—Test chitinous, often coloured, covered with amorphous scales which often overlap, thus giving it a faint, irregularly tessellated appearance; strongly compressed, broadly oval, with a wide and often convex mouth aperture in broad view, mouth narrow and appearing as a notch in side view.

Francé records *H. petricola*, Leidy (very numerous in some samples; found in arable soils, but not in woodlands or meadows), *H. picta*, Leidy, *H. rosea*, Penard, and *H. sylvatica*, Penard.

Amphizonella violacea, Greef.—Test homogeneous and membranous, showing a double contour, of which the outer is finely serrated; thinner and flexible around the mouth; colour violet; plasma very dense and granular; pseudopodia straight, digitate, and blunt; nucleus single. Average diameter 160 μ. Wolff, arable soil.

Family (ii.) *Euglyphina.* — *Test homogeneous or composed of chitinous or siliceous plates often of geometrical pattern; spinous or naked. Pseudopodia filose, simple or branched, of variable length and not anastomosing.*

Euglypha, Duj.—Test hyaline, more or less ovoid, composed of circular, oval, or scutiform siliceous imbricated scales arranged in longitudinal rows; mouth bordered with regularly arranged denticulate scales. Many of the known species have spines, but the soil forms are almost invariably glabrous.

E. tuberculata, Duj.—An uncompressed form, ovoid, narrower at mouth than at aboral end, scales circular or broadly oval; mouth circular and surrounded by finely serrate scales. Length 45 to 100 μ, greatest breadth 24 to 50 μ, aperture 10 to 20 μ, body scales 10 to 26 μ long (Plate V., Fig. 12).

Tristan da Cunha, ? Gough Island, Mauritius, Argentine, Congo, St Helena, Greenland. The forms found in some of these soils were considerably smaller than the measurements given above and belonged probably to the variety *minor* of Taranek.

The occasional references to *E. alveolata*, Duj., probably refer to this species, since Wailes regards *E. alveolata* as synonymous partly with this and partly with *E. acanthophora* (Ehrbg.) Perty, which so far has not been identified from soil. The references in question are Francé (widely distributed everywhere, typical of woodlands and meadows), Yakimoff and Zérèn (in most soils), Fantham and Taylor and Fantham and Paterson (not in water-logged soils).

E. mucronata, Leidy. — Another uncompressed form, more elongated than *E. tuberculata;* aboral end conical and generally provided with one or two terminal spines. Length 100 to 140 μ.

Francé (a glabrous form found in a Siberian soil).

E. bryophila, Brown.—Small (48 μ × 18 μ), ovoid, and slightly compressed, but mouth circular and surrounded by a row of five simple scales; tuft of spines at aboral end.

South Georgia. This is one of the very few records of a spined test in soil.

E. strigosa (Ehrbg.) Leidy.—Test compressed, broadly oviform or pyriform, elliptical in section but mouth circular; scales bordering the mouth denticulated and thicker than the body scales; generally with spines. Length 45 to 100 μ.

Spitsbergen (2, ? 3 soils), var. *glabra*. Francé.

E. rotunda, Wailes.—Small and oviform, slightly compressed, but mouth circular, aperture scales with a single denticulation and not thickened as in *E. strigosa;* length 22 to 52 μ.

South Georgia, ? Argentine.

This may be the species referred to by Francé as *E. globulosa*, and stated by him to be typical of woodland soils (especially primitive forests and beechwoods) but not found in meadows or arable fields.

E. lævis (Ehrbg.) Perty.—The smallest of the Euglyphas, length 18 to 20 μ, oviform, compressed, mouth also elliptical and bordered by a row of simple pointed (not serrated nor dentate) scales.

Tristan da Cunha, Gough Island, Spitsbergen, Canada, Congo, ? Greenland, ? Azores. Francé.

E. ciliata (Ehrbg.) Leidy.—Oviform, compressed, elliptical in section, typically provided with short cils especially along the sides; mouth elliptical with 8 to 14 aperture scales, each of which has 3 to 5 denticulations. Length 40 to 90 μ, breadth 24 to 60 μ, mouth 10 to 23 μ.

Two (? three) soils from Gough Island (var. *glabra*). Francé.

Unidentified species of *Euglypha* have been found in a number of other soils from Egypt, Tristan da Cunha, South Georgia, Gough Island, Spitsbergen, Greenland, Argentine and Congo, and have also been mentioned by the following observers: Müller (in peat), Martin and Lewin (two species, one from a cucumber bed, the other from a seedling bed), Francé (in both wet and dry soils), Nowikoff, Fantham and Taylor and Fantham and Paterson (widely distributed in South African soils, both water-logged and drained; an autumn, *i.e.*, April form in the Karroo).

Placocysta spinosa (Carter) Leidy.—Structure of test like that of *Euglypha*, but the pointed aperture scales are absent and the border of the mouth is smooth; test much compressed, mouth linear. Length 116 to 174 μ.

Francé (1921). This genus is generally found only in sphagnum and not in other mosses; its occurrence in soil is therefore most probably quite accidental.

Assulina muscora, Greef (= *A. minor*, Penard).—Test ovoid or sub-circular, often asymmetrical, compressed, composed of imbricated oval scales, colour generally brown, owing to presence of a thin chitinous lining; mouth bordered by an irregularly-dentate membrane. Length 28 to 58 μ.

South Georgia, Spitsbergen (3 soils).

Francé (found once only, under moss).

A. seminulum (Ehrbg.) Leidy.—A larger species; length 60 to 90 μ.

Francé (1921; scarce in deciduous woods and gardens; absent from meadows and arable fields).

Sphenoderia, Schlumberger.—Test colourless and hyaline, composed of regularly-imbricated plates, globular or ovoid; mouth either linear at the end of a short neck, or circular with a thin dentate lip.

S. lenta, Schlumb.—Test globular, scales numerous and almost circular, mouth linear. Length 30 to 64 μ.

Francé (1921; moorland soil).

S. fissirostris, Penard.—A smaller ovoid form also with a linear mouth, but with few relatively large scales arranged in four transverse rows.

Gough Island (in each of the five soils examined).

S. dentata (Moniez) Penard.—Test not compressed; mouth circular with a dentate chitinous lip, length 35 to 61 μ.

Gough Island (? *Euglypha tuberculata*).

Francé.

Campascus sp., Leidy.—Test retort-shaped with curved neck; aperture circular with a thin, disc-shaped collar; transverse section triangular with

rounded angles; composed of a chitinous pellicle covered with small irregularly arranged scales.

Francé. This is an aquatic and sphagnum form and probably only occurs accidentally in soil.

Trinema, Duj.—Small, colourless, hyaline tests composed of circular plates, mouth oblique or subterminal, invaginated.

T. enchelys (Ehrbg.) Leidy (= *T. acinus*, Duj.).—Test ovoid, tapering towards the mouth end; plates fairly easily visible. Length 30 to 100 μ (Plate V., Figs. 10, 11). Found in 32 soils from England, Spitsbergen, Greenland, South Georgia, Tristan da Cunha, Gough Island, St Helena, Mauritius, Argentine, Japan, Congo, Australia, and West Indies.

Goodey (manured arable soil), Wolff (arable soil), Francé (in practically all soils).

T. lineare, Penard.—A smaller form with scales not easily visible; length 18 to 35 μ. Also very widely distributed. Found in 26 soils from Spitsbergen, Greenland, Canada, South Georgia, Tristan da Cunha, Gough Island, St Helena, Mauritius, Argentine, India, and Ocean Island.

Francé (rarely absent in soils).

T. complanatum, Penard. — Test when seen in broad view not tapering but with parallel sides and semicircular ends; plates quite distinct. Length 25 to 60 μ, breadth 14 to 40 μ.

Azores, Greenland, ? South Georgia. Francé (woodland and meadow soils, not in arable soils).

Trinema sp. is also mentioned by Martin and Lewin as having been found in a cucumber bed.

Corythion dubium, Taranek.—Test somewhat like that of *Trinema lineare*, but composed of small oval plates which are not imbricated; length 23 to 65 μ. Gough Island. Francé (1921).

Family (iii.) *Gromiina.—Test membranous, usually flexible, smooth or covered with extraneous particles; pseudopodia long, branching, frequently anastomosing.*

Lecythium hyalinum (Ehrbg.) Hertwig and Lesser (= *Chlamydophrys stercoreum*, Cienk., *Pamphagus hyalinus*, Leidy, *Platoum stercoreum*, Bütschli).—Test very fine, homogeneous, and flexible; ovoid to spherical; pseudopodia long, fine, and branching; protoplasm divided into two fairly sharply distinguished zones, that near the mouth being granular and containing food bodies, etc., and that at the aboral end being very clear and containing a large easily visible nucleus. Length about 20 μ. This species has recently been revised by Belar,[9] who has divided it into five new species. It is not certain how many of these occur in the soil (Plate V., Fig. 5).

A very common soil organism found in 24 soils from all parts of the world. Martin ("sick" soils), Martin and Lewin (cucumber bed), Wolff (field soils), Goodey, Perey (3 out of 5 French soils), Yakimoff and Zérèn (7 out of 15 Russian soils), Allison (65 per cent. of U.S.A. soils), Francé.

L. mutabile (Bailey) Hopk.—A larger yellowish form compressed so as to be lenticular in section, aperture small, length 20 to 70 μ. Francé (1921), Fellers and Allison (rare).

Pseudodifflugia gracilis, Schlumb. — Test like that of *Lecythium*, but more rigid and covered with foreign bodies; broadly ovoid to sub-spherical, not compressed; nucleus at aboral end; length 20 to 65 μ (generally 30 to 40 μ). Francé (woodlands, not meadows or arable soil; very wet soils rich in humus).

The small organism described on p. 156 may belong to this genus (*? P. fulva* (Archer) Penard), the main differences being—

(1) The pseudopodia are long and filose in *Pseudodifflugia*.

(2) The test is colourless in cultures and has only cocci, etc., adhering to it (not soil particles as in *Pseudodifflugia*).

According to Wailes, however, some species of this genus are very variable.

Allogromia, Rhumb.—Test ovoid, fairly rigid, smooth or with a thin coating of foreign bodies, aperture terminal with long, fine, anastomosing pseudopodia arising from a short peduncle.

A. fluvialis (Duj.) Rhumb. (= *Gromia terricola*, Leidy).—Test ovoid to spherical, generally pale yellow in colour, length usually 80 to 120 μ.

Wolff (1912) (a "Leitform" in field soils).

Individuals of this genus (probably of the same species) were found in 2 soils from Gough Island and South Georgia, and were also observed in peat by Müller.

Microgromia, Hertwig and Lesser.—Tests small, hyaline, uncompressed, more or less spherical without extraneous adhering particles; mouth circular, terminal; pseudopodia fine, long, sometimes branching and anastomosing, usually arising from a small peduncle.

M. socialis (Archer) Hertwig and Lesser.—Test with a short neck, diameter 25 to 35 μ (Wailes). Many individuals often connected into colonies by the anastomosing pseudopodia. Fellers and Allison (rare, diameter 8 to 14 μ), Yakimoff and Zérèn (occasional, found in 4 out of 15 soils).

A somewhat similar form has been found in soils from Greenland, Tristan da Cunha, South Georgia, and ? St Paul's Rock. This form is spherical and very slightly elongated, usually about 15 to 17 μ long (occasionally only 12 μ), with circular mouth of diameter 5 μ; there is no neck, though a thickening of the test round the mouth sometimes gives an appearance as of a short neck. The nucleus is generally visible just behind the centre, and there are two contractile vacuoles also near the middle. All the individuals observed have been solitary.

Geococcus vulgaris, Francé.—A small organism which, pending further investigations, may be regarded as allied to *Microgromia*, since, according to Francé, it differs only in the fact that the pseudopodia (which were only once observed) are lobose instead of filose. Almost spherical, with a fairly thick, transparent, colourless wall; diameter 15 to 18 μ; slightly thickened around the mouth which is circular; protoplasm adheres to the test only at a few points; nucleus generally single, vesicular, contractile, vacuole generally at aboral end.

Francé (an exceedingly characteristic soil organism and found in very many soils, but especially in deciduous woods; absent from very dry soils).

Family (iv.) *Amphistomina.*—*Test membranous, chitinoid; pseudopodial openings at opposite poles.*

Diplophrys archeri, Barker. — Test a delicate hyaline membrane, spherical, with two apertures at opposite poles, from each of which very thin radiating pseudopodia arise. Diameter 8 to 20 μ.

Fellers and Allison (rare; diameter 20 to 35 μ).

Key to the Identification of the Soil Rhizopod Tests.

The method of using this key is identical with that already explained for the key to the soil flagellates.

Rhizopoda testacea.

A.—Structure of Test:—

(1) Homogeneous, membranous—

Arcella—brown or yellow; B 3, C 1, 2.
Pseudochlamys—young test colourless, old tests brown; B 1.
Corycia — young test colourless, old tests brown; B 1.
Parmulina—A 2, B 3, C 3.
Difflugiella—colourless; B 4, C 2.
Hyalosphenia—colourless, often covered with pits; B 4, 5, C 2.
Amphizonella—colourless and very thin; B 1, C 2.
Lecythium—colourless (yellow in *L. mutabile*) and very thin; B 4, C 2.
Microgromia—colourless; B 2, B 5, C 2.
Diplophrys—colourless; B 2, C 2.
Geococcus—colourless; B 2, C 2.

(2) Covered with sand grains and other extraneous matter—

Centropyxis—B 3, C 1, 2, 4.
Difflugia—B 2, 3, 4, 5, C 1, 2, 4.
Parmulina—A 1, B 3, C 3.
Phryganella—B 2, C 2.

A.—Structure of Test—*contd.*

(2) Covered with sand grains and other extraneous matter—*contd.*

Pseudodifflugia—B 4, C 2.
Allogromia—(usually) B 2, C 2.
Heleopera—sand grains at aboral end of test only; A 3 iii, B 4, C 5.

(3) Composed of, or covered with, plates—

(i) Plates oval, circular, or scutiform.
Euglypha—B 4, C 2, 6.
Placocysta—B 4, C 3.
Assulina—B 4, C 2, 6.
Sphenoderia—B 2, 4, 5, C 2, 3, 6.
Trinema—B 4, C 1, 2.
Corythion—B 4, C 1, 2.

(ii) Plates rectangular.
Quadrula—B 2, 4, C 2, 5.

(iii) Plates irregular.
Nebela—B 4, 5, C 2.
Heleopera—A 2, B 4, C 5.
Campascus—B 4, C 2.

B.—Shape of Test:—

(1) Discoid, saucer-shaped—

Pseudochlamys—A 1.
Corycia—A 1.
Amphizonella—A 1, C 2.

(2) Spherical—

Difflugia globula—A 2, C 2.
„ *lobostoma* (sometimes)—A 2, C 4.
Phryganella—A 2, C 2.
Quadrula irregularis (sometimes)—A 3 ii, C 2, 5.
Sphenoderia lenta—A 3 i, B 5, C 3.
Sphenoderia fissirostris—A 3 i, C 3.
Microgromia—A 1, B 5, C 2.
Diplophrys—two apertures at opposite poles; A 1, C 2.
Geococcus—A 1, C 2.
Allogromia—A 2, C 2.

B.—Shape of Test—*contd.*

(3) More or less hemispherical with aperture in the flattened or concave "ventral" surface—

Arcella—A 1, C 1, 2.
Centropyxis—asymmetrical, aperture excentric; A 2, C 1, 2, 4.
Difflugia arcula—A 2, C 4.
Difflugia craterella—A 2, C 1.
Parmulina—A 1, 2, C 3.

(4) More or less elongated, mouth terminal—

Difflugia (most species)—A 2, C 1, 2, 4.
Difflugiella—A 1, C 2.
Hyalosphenia—A 1, C 2.
Nebela—A 3 iii, B 5, C 2.
Quadrula—A 3 ii, C 2, 5.
Heleopera—A 2, 3 iii, C 5.
Euglypha—A 3 i, C 2, 6.
Placocysta—A 3 i, C 3.
Assulina—A 3 i, C 2, 6.
Sphenoderia—A 3 i, B 2, 5, C 2, 3, 6.
Campascus—retort-shaped; A 3 iii, C 2.
Trinema—mouth sub-terminal or ventral; A 3 i, C 1, 2.
Corythion—A 3 i, C 1, 2.
Lecythium—A 1, C 2.
Pseudodifflugia—A 2, C 2.

(5) With distinct neck—

Difflugia urceolata—A 2, B 2, C 2.
Hyalosphenia elegans—A 1, B 4, C 2.
Nebela—A 3 iii, B 4, C 2.
Sphenoderia lenta—A 3 iii, B 2, C 3.
Campascus—A 3 iii, B 4, C 2.
Microgromia socialis—neck very short; A 1, B 2, C 2.

C.—Aperture:—

(1) Invaginated—

Arcella—A 1, B 3.
Centropyxis lævigata—A 2, B 3, C 2, 4.
Difflugia constricta—A 2, B 4.
„ *craterella*—A 2, B 3.
Trinema—A 3 i, B 4.
Corythion—invagination slight; A 3 i, B 4.

C.—Aperture—*contd.*

(2) Circular to oval—

Arcella—A 1, B 3.
Centropyxis—A 2, B 3, C 4.
Difflugia globula—A 2, B 4.
Phyganella—A 2, B 2.
Difflugiella—A 1, B 4.
Hyalosphenia—A 1, B 4, 5.
Nebela—A 3 iii, B 4, 5.
Quadrula—A 3 ii, B 2, 4.
Amphizonella—A 1, B 1.
Euglypha—A 3 i, B 4, C 6.
Assulina—A 3 i, B 4, C 6.
Sphenoderia dentata—A 3 i, B 4.
Campascus—A 3 iii, B 4.
Trinema—A 3 i, B 4.
Corythion—A 3 i, B 4.
Lecythium—A 1, B 4.
Pseudodifflugia—A 2, B 4.
Allogromia—A 2, B 2.
Microgromia—A 1, B 2.
Diplophrys—A 1, B 2.
Geococcus—A 1, B 2.

(3) Linear—

Parmulina (mouth capable of being opened and closed)—A 1, 2, B 3.
Placocysta—A 3 i, B 2.
Sphenoderia lenta—A 3 i, B 2.
„ *fissirostris*—A 3 i, B 2.

(4) Outline lobed—

Difflugia arcula—A 2, B 3.
„ *lobostoma*—A 2, B 2.
Centropyxis (sometimes)—A 2, B 3, C 1, 2.

(5) Test in side view notched at the aperture—

Hyalosphenia minuta—A 1, B 4.
Quadrula irregularis—A 3 ii, B 2, 4.
Heleopera—A 2, 3 iii, B 4.

(6) Surrounded by teeth—

Euglypha—A 3 i, B 4, C 2.
Assulina—A 3 i, B 4, C 2.
Sphenoderia dentata—A 3 i, B 4.

Ciliata.

The classification adopted in the following pages is that used by Roux.[98]

ORDER 1. — HOLOTRICHA. CILIA ALL SIMILAR, AND GENERALLY DISTRIBUTED UNIFORMLY ALL OVER THE BODY.

Sub-order (i.) *Gymnostomata.—Mouth generally shut except during feeding; pharynx, if present, not provided with any supporting skeletal structures.*

A. *Prostomata.—Mouth at anterior end of body, pharynx tubular and often not easily visible.*

Family *Holophryna*, Perty.—*Body covered uniformly with cilia; no special appendages around the mouth.*

Holophrya, Ehrbg. — Shape symmetrical, cylindrical-ellipsoidal. Except in the absence of rods round the pharynx this genus is very like *Prorodon* and may easily be confused with it. Some species are obligate or facultative anaerobes.

H. ovum, Ehrbg.—Ovoid; length 120 μ, greatest width 90 μ.

Fantham and Taylor, Fantham and Paterson (in many South African soils of varying types).

Holophrya sp. was found in soils from Kenia, Egypt, Antigua, and England. Also recorded by Yakimoff and Zérèn (very frequent, found in 9 out of 15 soils), Wolff (field soils), Francé, Fellers, and Allison (probably several species). Losin-Losinsky found *H. discolor*, Ehrbg., and another species in steppe soils of Turkestan.

Urotricha, Clap. and Lach.—Small, symmetrical

ciliates, spherical to ellipsoidal; cilia arranged in regular rows more or less broken in the posterior region; one or more long cilia at posterior end; pharynx sometimes surrounded by rods; movements slow and irregular, sometimes jumpy.

U. farcta, Clap. and Lach.—Ovoid, narrow in front; length 24 μ, width 18 μ. Nowikoff. Commonly found where oxygen tension is low. Food is bacteria and fine detritus.[95]

U. agile, Stokes.—Fellers and Allison (occasional).

Urotricha sp., length 35 to 50 μ. Fellers and Allison.

Enchelys, Hill.—Like *Holophrya*, but anterior end drawn out to a neck; no pharynx.

The identification of the species of this genus is very uncertain, and the majority of authors are content with recording the genus. Superficially the form found in the soil shows considerable resemblance in size, shape, and mode of swimming to *Balantiophorus elongatus*, Schew., which is a common soil form, and consequently, since some of the authors who describe *Enchelys* sp. as being very common in the soil do not mention *Balantiophorus* at all, it is possible that the two organisms have often been confused. There is however no doubt that both occur in the soil with considerable frequency.

The common soil form is about 25 to 30 μ long, slightly less than half this in width, and tapers slightly towards the fore end, which is curved a little and obliquely truncated. Only slightly flexible; contractile vacuole at the posterior end; cilia fine and short. Larger forms up to 60 μ in length are sometimes found and these are often slightly flattened, though the smaller ones are practically circular in section.

Found in 41 of the soils from all parts of the

world. Fellers and Allison (*E. farcimen*, Ehrbg., one of the six commonest soil ciliates, length 30 to 60 μ; another species occasionally found). Yakimoff and Zérèn (? *E. farcimen;* fairly common; found in 8 out of 15 soils). Wolff (*E. pupa*, Ehrbg., in field soils). Waksman (*E. pupa*, one of the three commonest soil ciliates). Koch (? *E. pupa* in greenhouse soil). Goodey (occasionally found in arable and pasture soils). Lodge and Smith; Cunningham and Löhnis.

Spathidium spathula, O. F. M. (= *Leucophrys spatula*, Ehrbg.).—Differs from *Enchelys* in having a ring of longer cilia at the anterior end around the mouth, and an elongated (instead of ovoid or spherical) meganucleus; anterior end truncated squarely rather than obliquely. Length 180 to 200 μ, width 45 to 60 μ. A facultative anaerobe feeding on *Colpidium* and other small ciliates. Goodey (occasional in manured arable soil). Yakimoff and Zérèn (rare but recorded from 6 out of 15 soils; length 133 μ). Losin-Losinsky (Turkestan, heavy steppe soil).

Lacrymaria olor (O. F. M.).—Flask-shaped, with a long, flexible, slightly flattened neck; hind end pointed; very contractile; mouth situated in a small conical projection at the end of the neck, surrounded by a ring of long cilia; macronucleus double, each part ovoid, cilia arranged in spiral rows; length when extended 350 to 400 μ.

Nowikoff (well-manured soils). Fantham and Taylor, Fantham and Paterson (in many South African soils). Fantham and Paterson also found

an unidentified species (? *L. cohni*) in a single, long-cultivated soil.

Prorodon teres, Ehrbg.—Shape ellipsoidal, not compressed, ends equally rounded; cilia fine and short, arranged in longitudinal rows; mouth terminal or very slightly subterminal, leading to a pharynx surrounded by rod-like structures; macronucleus spherical or elongated; contractile vacuole posterior; movements regular, fairly rapid and spiral; length 80 to 200 μ, width 50 to 140 μ.

Wolff (field soils), Fellers and Allison (occasional, a small form, length 60 to 150 μ), Yakimoff and Zérèn (once only in a vegetable garden soil). A very similar species, *P. ovum*, Ehrbg., has been recorded by Wolff (field soils), Koch, Waksman and Fantham and Taylor (once only). Fellers and Allison record another unidentified species of the same genus.

Chœnia, Quenn.—An organism which probably belongs to this genus, but which has not been identified with any of the established species, has been found in soils from Spitsbergen, Egypt, South Africa, Mauritius, Ocean Island, and Tristan da Cunha. It is an elongated organism, length about 120 μ, greatest width about 15 μ, tapering slightly to a neck in front but with the extreme anterior end slightly broader again and squarely truncated; posterior end not pointed; body not compressed. Cilia arranged in longitudinal rows and slightly longer at the anterior end; body flexible but not contractile; mouth at the anterior end; usually with numerous vacuoles in the middle and posterior parts of the

body. It swims rather slowly either backwards or forwards.

Family *Colepina*, Ehrbg. — *Body generally enclosed in a carapace; cilia uniformly arranged in longitudinal rows, longer and stouter round the mouth.*

Coleps hirtus (O. F. M.) Ehrbg.—Barrel-shaped, symmetrical, covered with elongated plates; three hook-like processes at the hinder end; mouth terminal, surrounded by a ring of longer cilia. Macronucleus ovoid, central, size about 38 to 46 μ by 18 to 30 μ. This species is quite unmistakable, but is rare in soil, having only been found by Fantham and Taylor (in several different soils) and Yakimoff and Zérèn (in one soil only).

This scarcity is rather strange in view of the statement by Noland[84] that "probably no other ciliate is able to live in a wider variety of habitats, or is able to subsist on a more varied diet, than *Coleps hirtus*." It occurs in both salt and fresh water, and can tolerate a considerable shortage of oxygen, but is said to be susceptible to CO_2. Elsewhere Noland describes it as a warm water form developing poorly in cool cultures and feeding mainly on euglenoids.[85]

Family *Cyclodina*, Stein. — *Holotrichous ciliates having at the anterior end one or more rings of long, silky but strong membranellæ, in which the individual cilia are often separate.*

Mesodinium sp. Stein.—Shape spherical to ovoid with a transverse groove near the anterior end dividing the animal into two unequal parts. Cilia absent from all parts of the body except this groove in which are inserted one or more rings of long membranellæ. Mouth at the apex of the short conical anterior part, leading to a pharynx provided with rods.

Fellers and Allison. This is the only record of any member of this family in soil, and the authors themselves query their identification.

B. Pleurostomata.—Mouth either a groove along the anterior part of one lateral side or else circular and ventral; shape of body generally less symmetrical than among the Prostomata, often laterally compressed and often prolonged into a snout overhanging the mouth.

Family *Amphileptina*, Bütschli. *Body more or less compressed laterally with buccal groove at the anterior end of the narrow ventral edge; cilia either uniformly distributed or confined to one of the lateral surfaces.*

Amphileptus, Ehrbg. — Compression very slight and limited to the anterior end, which is drawn out and obliquely truncated; cilia distributed uniformly in longitudinal rows all over the body, usually rather longer round the buccal groove. Macronucleus composed of two spherical or ellipsoidal masses (cf. *Dileptus*). Among the largest of the soil ciliates.

A. cygnus, Clap. and Lach.—Distinguished by a long ribbon-like trunk with the mouth and contractile vacuole at its base; length (omitting neck) 200μ.

Fantham and Taylor, Fantham and Paterson (in several non-water-logged soils).

A. gigas (Clap. and Lach.). — Fantham and Paterson (once only).

Lionotus fasciola, Ehrbg.—Neck not so distinct as in *Amphileptus*, and body more flattened; cilia in longitudinal rows on one side only; length 80 to 100μ; macronucleus consisting of two ellipsoidal masses.

Fellers and Allison (occasional). Fantham and Taylor, Fantham and Paterson (in several South African soils).

Loxophyllum, Duj.—Body very strongly flattened, leaf-like, generally tapering and curved in front, flexible and contractile; cilia on one surface only and arranged in longitudinal rows.

Fellers and Allison (*L. flexilis*, occasional; length 70 to 150 μ). Fantham and Taylor, and Fantham and Paterson (*L. rostratum* in a few South African soils).

Family *Trachelina* (Ehrbg.) Stein. — *Anterior end drawn out to a trunk with a circular mouth at the base; pharynx with an armature of little rods; ciliation uniform all over the body, but with special cilia on the ventral surface of the trunk.*

Dileptus, Duj.—Very similar to *Amphileptus*, but with the characters of the family; trunk flattened and very flexible; macronucleus moniliform; contractile vacuoles numerous, situated along the dorsal surface; a row of big trichocysts along the ventral edge of the trunk, together with a row of cilia. Food, small ciliates. In natural waters it is commonly found where oxygen is deficient.[85]

Australia (New South Wales). Lodge and Smith, Gainey, Fellers and Allison (*D. gigas*, length 200 to 700 μ and another species; both occasional). Yakimoff and Zérèn (in 1 soil only out of 15, length 300 μ). Losin-Losinsky (? *D. gigas*, heavy steppe soil, Turkestan).

Family *Nassulina*, Bütschli. — *Ovoid or ellipsoidal; no trunk; ciliation uniform; mouth round*

and situated on ventral surface in anterior half of body; with an adoral ring of long, stout cilia; pharynx rather long and surrounded with rods.

Nassula elegans, Ehrbg.—Ovoid, broadest behind, and slightly curved in front, both ends rounded, slightly flattened dorso-ventrally; pharynx long and somewhat dilated at the anterior end; macronucleus ovoid and central; contractile vacuole surrounded with secondary vacuoles near centre of body; often coloured; length 100 to 140 μ.

Wolff (common in field soils), Koch (? in greenhouse soils), Waksman, Nowikoff, Fantham and Paterson (in a single South African soil).

B. Hypostomata.—Mouth on the ventral surface; cilia confined to ventral surface; generally oval to bean-shaped and flattened.

Chilodon, Ehrbg.—Body flattened, especially at the sides and anterior end, and asymmetrical; mouth median, pharynx well-developed, conical, and surrounded with rods; cilia in longitudinal rows.

C. cucullulus (O. F. M.)—Length 50 to 150 μ, with several contractile vacuoles (Plate VI., Fig. 5).

Fellers and Allison (occasional; length 70 to 150 μ). Fantham and Paterson (in a few South African soils of various kinds).

The other species recorded from the soil differ from this mainly in being rather smaller in size. They are—

C. megalotrocha, Stokes. — Fellers and Allison (common).

C. uncinatus, Ehrbg.—Yakimoff and Zérèn (fairly

frequent, found in 7 out of 15 soils; average size about 45μ × 30μ).

Small forms similar to these latter were found in soils from Tristan da Cunha, Cape Verde Island, Spitsbergen, Mauritius, and Serbia, and other unidentified forms have been recorded by Martin and Lewin (in cucumber beds), Goodey (fairly common in arable and pasture soils), Waksman and Nowikoff.

Family *Dysterina*, Clap. and Lach. — *Cilia usually cover only part of the ventral surface; spiny process present at posterior end.*

Trochilia palustris, Stein.—A small dorsoventrally flattened, oval-shaped ciliate, obliquely truncated at the anterior end; cilia in longitudinal rows limited to a median band on the ventral surface; pharynx long, conical, and without rods; mouth in anterior half of ventral surface; macronucleus ellipsoidal and central; contractile vacuoles one or two; one of the cilia at the anterior end is longer and stouter than the others, forming an anterior spine, and there is a larger pointed mobile appendage at the posterior end. Length 35μ, breadth 20μ.

Wolff (field soil). A ciliate very like this was found in cultures of soils from Greenland, Mauritius, and Gough Island, but accurate identification was impossible in each case. According to Noland,[85] *T. palustris* is essentially a cold-water form, never occurring in nature in waters with temperatures above 15.5° C., and rapidly dying when brought into a warm room.

Sub-order ii. *Trichostomata.—Mouth permanently*

open with a row of cilia or one to two undulating membranes along the outer margin.

Family (a).—*No peristome; undulating membranes small or absent; cilia generally fine and short.*

Uronema marina, Duj.—Elongated ellipsoidal in shape, with slight lateral compression; cilia arranged uniformly in longitudinal rows; a single long bristle at the posterior end; mouth a longitudinal oval opening on the ventral surface in the anterior part of the body with a row of closely set cilia on the right-hand edge and an undulating membrane on the left; no pharynx; macronucleus spherical, central; contractile vacuole single, posterior; movements rapid, rotating on the long axis. Length 30 to 60 μ. Spitsbergen (one soil only). Wolff (field soils), Fellers and Allison (occasional, length 22 to 40 μ), Yakimoff and Zérèn (in 2 out of 15 soils).

Waksman records *Uronema* sp.

Buddenbrock[13] has recently divided this genus into three species. It is at present uncertain which of these is the one found in the soil.

Cryptochilum nigricans (O. F. M.) Maupas.—Very like *Uronema* and with a similar long caudal bristle inserted obliquely; ventral surface with a shallow longitudinal furrow running from the anterior end to near the middle of the body; mouth situated at the end of this furrow, small, and provided with small undulating membranes; movements irregular; length 12 to 50 μ. The difference between this genus and *Uronema* is very slight, and Bütschli regards them as identical.

Goodey (fairly common in a manured arable soil).

Glaucoma, Ehrbg.—Very like the two preceding species, but with a short, shallow pharynx containing an undulating membrane; slightly flattened dorso-ventrally; ciliation uniform all over the body, but rows closer together than in *Cryptochilum*; caudal bristle absent from the soil species; mouth ventral, elliptical and set longitudinally in front of the middle, with an undulating membrane that is constantly in motion, and which extends all round the left-hand and anterior borders and part of the right-hand border; macronucleus spherical, central; contractile vacuole single, posterior; movements rapid, uninterrupted, with rotation on the long axis. Food, bacteria and fine detritus. Can tolerate high pressure of carbon dioxide.[85]

G. scintillans, Ehrbg.—Length 60 to 86μ (Plate VI., Fig. 8). Wolff (a "Leitform" in field soils). Fellers and Allison (common; length 40 to 100μ). Yakimoff and Zérèn (in 1 soil out of 15).

G. pyriformis, Ehrbg.—A rather smaller species, somewhat narrower in front than *G. scintillans*, and with the undulating membrane better developed on the right-hand side of the mouth. A facultative anaerobe. Wolff (field soils).

Glaucoma sp. has also been recorded by Koch (greenhouse soil), Waksman, Fellers and Allison (*Trichoda pura*, occasional), and was found here once in a soil from Barbadoes.

Colpidium, Stein.—Shape ovoid with slight dorso-ventral flattening, hind end rounded, and anterior

end rather narrower and curved ventrally, causing a concavity near the anterior end of the ventral surface; mouth oval, set obliquely at the bottom of this concavity with a narrow undulating membrane on both sides; pharynx long, with an undulating membrane; macronucleus large, ellipsoidal, and central; contractile vacuole single, at or just behind the middle of body; cilia arranged uniformly in longitudinal rows. This genus was only found in a few of the soils examined here, namely, one soil each from Gough Island, Mauritius, Greenland, ? St Helena, ? Ocean Island. Other authors, however, found it much more frequently, but as many of them do not mention *Balantiophorus*, which is a common and very similar form, it is possible that some of their records refer to this latter genus. A facultative anærobe developing abundantly where oxygen is deficient.[85]

C. colpoda, Stein.—Wolff (common in field soils), Cunningham and Löhnis, Koch (greenhouse soil), Waksman (one of the three commonest soil ciliates), Fellers and Allison (?—common), Fantham and Taylor (in a single soil), Fantham and Paterson (in many cultivated and uncultivated soils), Nowikoff, Yakimoff and Zérèn (in 6 out of 15 soils). Length 30 to 45μ. (Plate VI., Fig. 4.)

C. striatum, Stokes.—Fellers and Allison (common, length 45 to 75μ), Fantham and Taylor and Fantham and Paterson (in many drained soils and a few water-logged soils).

Colpidium sp.—Bréal[12]; this record is of interest, as it is probably the earliest in which the function

of protozoa in the soil is considered. Bréal claimed that *Colpidium* was associated with ammonia formation in the soil and with the decomposition of plant remains. Taylor and Burns (in Egypt).

Colpoda, Ehrbg. — Shape reniform; somewhat compressed laterally, dorsal surface curved, ventral surface more or less straight, with a deep depression in the anterior or median part; mouth at base of this depression with a little tuft of longer cilia that often looks something like an undulating membrane; pharynx short; ciliation uniform in longitudinal rows; contractile vacuole single, posterior.

C. cucullus (O. F. M.) and *C. steinii*, Maupas, are the two commonest soil ciliates. The former was found in 83 and the latter in 70 of the 148 soils examined, and they have also been recorded by practically every investigator who has worked on this subject. *C. cucullus* is a large form, 40 to 80 μ in length, with the part behind the mouth very swollen and almost globular, while *C. steinii* is smaller (length 25 to 60 μ) and not inflated behind, so that the ventral surface is quite flat except for the notch which leads to the mouth; the anterior end is also more pointed than in *C. cucullus* (Plate VI., Figs. 1, 3). Both species are facultative anærobes.

C. maupasii, Enriques.—A more elongated form than *C. steinii*, with anterior end more rounded (Plate VI., Fig. 2).

Nine soils from Mauritius, Argentine, India (3), Ocean Island, Barbadoes, Congo (2), and Algeria.

Goodey (Rothamsted soils). Enriques[34] distinguished as follows between these three species :—

C. cucullus : number of frontal dentations (*i.e.*, transverse ridges in front of mouth) 9 to 10 ; macronucleus with a lobed karyosome.

C. steinii: frontal dentations 6 to 7; karyosome lobed.

C. maupasii : frontal dentations 6 to 7 ; karyosome spherical or ellipsoidal, not lobed.

The cysts of *C. cucullus* and *C. steinii* are very similar except in size, the former being on the average about 35 μ in diameter, and the latter 25 μ. Reproduction often occurs in the cysts, and just before excystation it is not uncommon to find cysts in which two or four individuals are actively rotating (Plate I., Fig. 23).

The cysts of *C. maupasii* are rather smaller, being generally about 15 to 20 μ in diameter, and are enclosed in a thick, structureless, mucilaginous outer layer, which is not so corrugated as the outer wall of the other species (Plate I., Fig. 24). In older cysts this outer layer condenses into a relatively thin and highly refringent wall.

Other species recorded from the soil are :—

C. campyla, Stokes. — Fellers and Allison (occasional).

C. flavicans, Stokes.—Fellers and Allison (rare).

C. helia, Stokes.—Fellers and Allison (occasional).

C. (*Tillina*) *saprophila*, Stokes.—Common, length 25 to 40μ—the figure of this species given by Fellers and Allison resembles closely *C. steinii*, which is not mentioned by them.

Paramœcium, O. F. M.—Shape elongated ovoid with a ventral ciliated groove (generally oblique) leading to the mouth; ciliation uniform all over body; no undulating membranes nor special cilia.

The complete absence of this common infusorian form from all the local and foreign soils examined at Rothamsted has already been commented upon. A number of records of *Paramœcium* from soils can however be found, but though some of these records are undoubtedly reliable, one cannot resist a suspicion that for the general soil investigator whose knowledge of systematic protozoology is limited to that derived from a course in general biology, there is a great tendency for any elongated, ovoid holotrichous ciliate to be called "*Paramœcium*."

P. aurelia, O. F. M.—Fantham and Taylor, Fantham and Paterson (several soils from all parts of South Africa), Nowikoff (well-manured soils).

P. bursaria, Ehrbg.—Noland[85] states that this species appears to be favoured by a combination of fairly low temperature, soft water, and high oxygen tension. Fantham and Paterson (once only—Pretoria).

P. caudatum, Ehrbg.—Tolerates low oxygen tensions.[85] Fellers and Allison (rare), Nowikoff (well-manured soils), Fantham and Paterson (a few South African soils). Nowikoff obtained this species from a soil, which had been stored dry for ten years, on addition of sterile water, which suggests strongly that, contrary to general experience, this species can encyst in the soil.

P. putrinum, Clap. and Lach.—Wolff (field soils), Fantham and Taylor, Fantham and Paterson.

P. trichium, Stokes.—Fellers and Allison.

Paramœcium sp.—Piettre and de Souza,[93] Lodge and Smith, Koch (probably the commonest of the larger protozoa in greenhouse soils), Waksman, Taylor and Burns, Fantham and Paterson.

Family (b) *Pleuronema*, Bütochli.—*Peristome large, longitudinal, and occupying the greater part of the ventral surface; undulating membrane along the edge of peristome also very big; cilia generally long.*

Pleuronema, Duj. — Ovoid with rounded ends, slightly compressed laterally; peristome with big undulating membrane occupying about three-quarters of the ventral surface; undulating membrane sometimes withdrawn into pharynx while animal is not feeding; mouth at posterior end of peristome without pharynx; macronucleus spherical, in front of middle of body; contractile vacuole single in a postero-dorsal position; cilia very long.

Not common in soils.

P. chrysalis, Ehrbg.—Fellers and Allison (occasional, length 30 to 70 μ). Wolff (field soils). Fantham and Taylor (several soils). Fantham and Paterson (one soil only).

Pleuronema sp.—Fellers and Allison (occasional). Waksman and Nowikoff (well-manured soils). A few individuals probably of this genus were found in cultures from 3 soils from England, Burma, and Egypt.

Cyclidium glaucoma (O. F. M.).—Very like *Pleuronema* but much smaller (18 to 24 μ), and with a caudal

cilium longer than all the others (this is not present in *Pleuronema*); cilia arranged rather sparsely; movements very rapid, and it often makes a sudden violent jump. Length 18 to 24 μ (Plate VI., Fig. 6).

Found in 11 soils from South Georgia, Gough Island (2), San Miguel, Spitsbergen (2), Greenland (2), Mauritius (2), Ocean Island. Wolff ("*Pleuronema glaucoma*, O. F. M.," in field soils). Fellers and Allison (common). Fantham and Taylor and Fantham and Paterson (very widely distributed; an autumn, *i.e.* April form in the Karroo soils). Yakimoff and Zérèn (in every one of the 15 soils examined: elsewhere in the same paper, however, it is referred to as being found very rarely in soil). Francé records *Cyclidium* sp.

Balantiophorus, Schewiakoff.—Peristome occupies only the anterior part of the ventral surface of the body; macronucleus ovoid, central; contractile vacuole single, posterior; dorsal surface convex, ventral surface flatter and truncated in front so that the anterior end of the body overhangs the peristome; undulating membrane can be withdrawn into the peristome.

B. elongatus, Schew.—Shape elongated and rather narrow; cilia long, sparsely scattered, and not arranged in distinct rows. Length 28 to 30 μ, breadth 10 μ (Plate VI., Fig. 7). A common soil ciliate. Found in 36 soils, from Tristan da Cunha (4), Mauritius (7), Argentine (2), Greenland (2), India (6), Canada. Sudan (2), Japan (2), Ocean Island (2), Congo (2), Barbadoes, Serbia, Australia, Algeria. Goodey (fairly common in arable and pasture soils), Cunningham and Löhnis, Sherman.

B. minutus, Schew.—Shorter and broader than *B. elongatus;* cilia more numerous and arranged in distinct longitudinal rows.

In 14 soils from St Helena, Gough Island (3), Spitsbergen, Greenland (2), Argentine (2), India (3), Congo, South Africa. Goodey (once only), Wolff (common in field soils).

Unidentified species of *Balantiophorus* were found in soils from Egypt (3), South Georgia and Argentine, and have been recorded by Cunningham and Goodey.[53]

Lembus pusillus (Quenn) Calkins.—Elongated and narrow, especially the anterior half which forms a narrow neck; not compressed; very flexible; peristome reaching from the anterior end to the mouth which is at or just behind the middle, and with an undulating membrane on either side; contractile vacuole single at posterior end. Length up to 100 μ, breadth about $\frac{1}{5}$ length. ? Fellers and Allison (rare).

Anophys sarcophaga, Cohn. — Like *Lembus* but shorter, and, although tapering and somewhat pointed in front, not drawn out into a neck; peristome also shorter. Fantham and Paterson (once only).

ORDER 2.—HETEROTRICHA. CILIATES WITH A SPIRAL ADORAL ZONE OF STOUT CILIA OR CIRRI LEADING TO THE MOUTH; UNDULATING MEMBRANE INSIDE MOUTH, OFTEN STRONGLY DEVELOPED; REST OF BODY COVERED UNIFORMLY WITH FINE CILIA.

Blepharisma sp., Perty.—Body elongated, very compressed, with anterior end rather pointed and curved to the left, and generally rounded at posterior

end; peristome narrow, extending nearly to middle of body, and leading to mouth and short pharynx; cilia long and fine, in longitudinal rows; contractile vacuole single, terminal; commonly found in waters with low oxygen tension; food, bacteria.[85] Length very variable: those found in soil cultures were about 65 to 75 μ long. Spitsbergen, Greenland, Mauritius. Fellers and Allison (? *B. ovata*, Stokes, length 80 to 150 μ; rare). Losin-Losinsky (Turkestan, heavy steppe soil).

Metopus, Clap. and Lach.—Shape very variable but characterised by a spiral twist of the anterior part of the body; some dorso-ventral flattening; very contractile; peristome reaches to middle of body with adoral zone well developed; mouth with fairly long pharynx; macronucleus ovoid. A warm-water form and facultative anærobe; food, bacteria.[85]

Fellers and Allison (*M. sigmoides*, Clap. and Lach. Length 90 to 160 μ; occasional).

Metopides acuminata, Stokes.—Like *Metopus* with anterior end twisted, but shape persistent; ovate to pear-shaped with broad end in front. Length about 73 μ.

? Fellers and Allison (rare).

Spirostomum ambiguum, Ehrbg. — Very narrow and elongated, rounded at ends, flexible and contractile; peristome running backwards to rather beyond the middle of the body; no undulating membrane; adoral cilia well developed; cilia on rest of body long and fine and arranged in longitudinal rows; contractile vacuole single, large, posterior;

macronucleus moniliform. Length extremely variable, 500 μ to 4 mm.

Fantham and Taylor and Fantham and Paterson (in a very few soils).

Condylostoma, Duj. — Body ovate to elongate, slightly flattened dorsoventrally; peristome well developed and broader than in the other members of this order; a large, undulating membrane along the right border of the peristome and a row of membranellæ around the anterior and left borders; cilia on other parts of the body short and fine in longitudinal rows; macronucleus moniliform.

Koch (? *C. patens;* garden soil).

ORDER 3. — OLIGOTRICHA. SMALL SPHERICAL OR CONICAL CILIATES WITH ADORAL ZONE AS IN THE HETEROTRICHA BUT OFTEN FORMING A CLOSED RING; CILIA USUALLY COMPLETELY ABSENT FROM OTHER PARTS OF THE BODY.

Strombilidium gyrans, Stokes.—Pyriform, broad end in front, tapering behind to a short tail, which forms an adhesive organ; adoral row of long stout membranellæ forming a complete ring round the flattened anterior end; macronucleus a transverse band broadest at the ends; contractile vacuole single, posterior; movements very rapid and violent, sometimes adhering by the posterior end and spinning rapidly around. Length 60 μ.

Wolff (field soils).

Strombidium, Clap. and Lach.—Shape roughly spherical or broadly ovoid; peristome large and extending to the ventral surface of the body; a few

scattered cilia on ventral surface; movements very rapid; requires good aeration.

Gainey, Lodge and Smith, Waksman, ? Fellers and Allison (rare, length 30 to 60 μ), Fantham and Paterson (in one soil only).

Halteria, Clap. and Lach.—Spherical, very like *Strombidium* but with an equatorial ring of long fine bristles; movements springing and erratic.

H. grandinella (O. F. M.).—Length 30 to 40 μ. A warm-water form (Plate VI., Fig. 9). Wolff (field soils). Fellers and Allison (length 25 to 35 μ, common), Fantham and Taylor, Fantham and Paterson, Yakimoff and Zérèn (in 3 out of 15 soils).

Halteria sp.—St Helena, Australia, Japan. Lodge and Smith, Waksman, ? Francé, Nowikoff, Losin-Losinsky (Turkestan, steppe soil).

ORDER 4.—HYPOTRICHA. DORSOVENTRALLY FLATTENED WITH CILIA ON THE VENTRAL SURFACE ONLY AND GENERALLY FUSED TOGETHER TO FORM CIRRI; ADORAL ZONE OF MEMBRANELLÆ PRESENT; TYPICALLY OF CREEPING HABIT.

Family (i.) *Oxytrichina* (Ehrbg.) Stein.—*Shape variable; ventral cirri in more or less numerous rows, often with additional isolated cirri, the difference between the kinds of cirri being generally well marked; macronucleus in rounded masses of variable number; never ribbon-like.*

(a) *Urostylinæ*, Bütschli. — Ventral cirri well developed, in two or more rows (one only in *Stichotricha secunda*); marginal cirri well developed and uninterrupted at the posterior end.

Urostyla grandis, Ehrbg.—A very large ciliate,

elongated but not tapering, and with ends equally rounded; peristome large, occupying practically the whole of the anterior part of the body; marginal, frontal, and 10 to 12 anal cirri well developed; five or more rows of ventral cirri, no caudal bristles; macronucleus composed of numerous small rounded masses difficult to see. Length 300 to 500 μ, width 120 to 180 μ.

This species may easily be confused with *Onychodromus*, from which it can be distinguished by the greater number of rows of ventral cirri.

Goodey (well-manured arable soil), Yakimoff and Zérèn (vegetable garden soil).

Urostyla sp.—Nowikoff.

Stichotricha secunda, Perty.—Elongated, anterior half very narrow and compressed and forming a contractile neck; peristome reaches to the middle of the body; adoral membranellæ well developed; no special frontal or anal cirri and no caudal bristles; single row of ventral cirri running obliquely from anterior end to near the posterior end; macronucleus composed of two separate ovoid masses. Length 100 to 200 μ. Food, diatoms and other algæ; requires good aeration.

Fellers and Allison (rare).

Uroleptus (Ehrbg.) Stein.—Elongated, rounded in front and pointed or drawn out to a tail behind; generally two rows of ventral cirri and three frontal cirri; no anal cirri and no caudal bristles; marginal cirri well developed but inserted a little on the ventral surface.

U. musculus, Ehrbg. — Tail short and conical, body broadest just behind the middle, maximum width equal to about $\frac{1}{3}$ length, anterior end curving slightly to the left and posterior end to the right; peristome occupying about $\frac{1}{3}$ of the body-length; marginal setæ set on the ventral surface a little in from the margin except at the hind end. Length 120 to 130 μ (Plate VI., Fig. 13). Greenland. Wolff (field soils), Koch (? greenhouse soils), Fellers and Allison (rare), Nowikoff, Yakimoff and Zérèn (?, in 2 out of 15 soils).

U. mobilis, Englm. — Very narrow, width only about $\frac{1}{12}$ length; hind end tapering to a blunt point; body cylindrical and contractile; peristome small, occupying only about $\frac{1}{9}$ of the body-length; marginal setæ relatively long and widely spaced; macronucleus consisting of six ovoid masses arranged in a longitudinal row. Length 350 to 400 μ.

Spitsbergen, ? Coimbatore (India).

U. piscis, Ehrbg.—A very large species; maximum width is at the middle of the body and equal to about $\frac{1}{6}$ or $\frac{1}{8}$ of the length; with a long, strap-like tail ending in a blunt point and turning to the right; anterior end rounded; very elastic; peristome occupying about $\frac{1}{4}$ to $\frac{1}{3}$ of the total length; marginal setæ set on ventral surface but project beyond the edge all along the body, rather longer on the tail; macronucleus consisting of two ovoid masses. Length 600 to 800 μ.

Mauritius (2), Coimbatore, ? St Vincent. Fantham and Taylor, Fantham and Paterson.

Uroleptus dispar, Stokes.—? Fellers and Allison (length 125 to 200 μ), Nowikoff, Fantham and Paterson (once only).

Uroleptus sp.—Ocean Island (2 ? *U. violaceus*) ? Japan, ? Australia. Waksman.

(b) *Pleurotrichinæ*, Bütschli.—Frontal cirri strong, usually 8; ventral cirri scattered or in a few, usually one or two, rows; marginal cirri well developed but often replaced by caudal bristles at the posterior end; anal cirri generally well developed.

Onychodromus grandis, Stein.—Broad, with parallel sides, almost rectangular, width about $\frac{2}{3}$ length; not flexible; peristome large and triangular, extending to the middle of the body; marginal setæ short, forming a continuous row except round the peristome region; 16 to 28 frontal styles arranged in three rows; 15 to 21 ventral styles arranged in three to four rows; 5 to 7 long straight anal styles; macronucleus consisting of four to eight ovoid masses. Length 100 to 350 μ.

The cyst is colourless and spherical, with a thick corrugated outer wall; outside diameter 54 μ, inside diameter 45 μ.

As already mentioned, this species is somewhat like *Urostyla grandis* and it can also be confused with *Gastrostyla steinii*, in which however the peristome is shorter and there is only a single row of ventral cirri.

Tristan da Cunha. Jameson [61] (garden soil), Taylor and Burns.

Gastrostyla, Englm.—Shape oval, peristome occupying about $\frac{1}{3}$ of the body-length; a single oblique row

of ventral cirri sometimes with a few additional scattered ones; marginal cirri uninterrupted at posterior end where they are generally a little longer; 5 to 6 anal styles; macronucleus in two or four ovoid masses.

G. steinii, Englm.—A large and broad species; length 150 to 300 μ, width 47 to 100 μ.

? Egypt. Goodey (twice in arable soil).

Gastrostyla sp.—? Canada. Taylor and Burns.

Gonostomum (*Plagiotricha*) *affine* (Stein.).—Elongated, ends equally rounded, section almost circular; very flexible; peristome reaching to the middle of the body, running back almost parallel to the axis of the body for the greater part of its length and making a very characteristic sharp bend inwards near the hind end; 5 or 6 ventral cirri arranged in an oblique row; marginal cirri as in *Gastrostyla*; 5 short and inconspicuous anal styles; macronucleus in two rather elongated ovoid masses. Length about 75 μ (Plate VI., Fig. 15). The cyst (Plate I., Fig. 25) has a thin smooth wall, diameter 33 μ. A very common soil form. Found in 24 soils from all regions. Goodey (widely distributed in arable and pasture soils). Emmerich, Leiningen and Loew, Perey, Allison (= "*Gastrostylis*" in 50 per cent. of the U.S.A. soils). Yakimoff and Zérèn (? = *Oxytricha affinis* in 7 out of 15 soils).

Oxytricha, Ehrbg.—Shape elliptical, ventral surface flattened, ends rounded, very flexible; ventral cirri 5, not arranged in a row; anal cirri 5, well developed.

O. fallax, Stein. — Flattened, egg-shaped, with narrower end in front; easily distinguished from *Stylonychia* by its great contractibility and flexibility. Length 150 to 170 μ, width 60 μ. ? Argentine, ? Rothamsted.

A very similar species, *O. bifaria*, Stokes, has been found by Fellers and Allison.

O. pellionella (O. F. M.). — A smaller species; elongated, not tapering, ends equally rounded; peristome reaching to about $\frac{1}{3}$ of the length; macronucleus in two ovoid masses (Plate VI., Fig. 14). Length 80 to 100 μ, width 19 to 24 μ. A cold-water form requiring high oxygen tension. Spitsbergen (2), Greenland, Punjab. Cunningham and Löhnis, Fellers and Allison (common), Fantham and Taylor, Fantham and Paterson.

Oxytricha sp.—England, Mauritius, Argentine, Ocean Island, Australia. ?, Goodey (manured garden soil), Piettre and Souza, Lodge and Smith, Waksman, Sherman, Nowikoff (well-manured soils).

Pleurotricha, Stein.—Like *Gastrostyla*, but with two or more rows of ventral cirri in addition to a median group of 4 to 5 cirri; shape persistent, not flexible.

P. lanceolata, Ehrbg. — One complete row of ventral cirri and a second incomplete row. Length 70 to 80 μ. The cyst of this species is characteristic, being covered with short, stout, straight spiny processes (Plate VI., Fig. 12).

A fairly common soil form, found in 15 soils from Palestine, Egypt (2), West Indies, ? Tristan da

Cunha, Spitsbergen, ? Argentine, ? Japan, ? India, South Africa, ? Canada, England. Goodey (? arable soil).

P. grandis, Stein.—A larger and broader species, widest a little behind the middle; peristome extending nearly to the middle; two complete and one partial row of ventral cirri on either side of the median group; macronucleus in two ovoid masses. Length 210 to 420 μ.

Organisms probably belonging to this species were found in cultures from soils from Assam, Punjab, and Canada. Goodey also records this species but queries the identification. Without careful examination it can easily be confused with large specimens of *Oxytricha fallax*.

Pleurotricha sp.—Goodey, Waksman, Nowikoff.

Stylonychia, Ehrbg.—Shape rather variable, ventral surface flat; peristome well developed; three characteristic long caudal bristles; macronucleus consisting of two ovoid masses; cirri usually very strong; ventral cirri 5, not arranged in a row.

S. mytilus, Ehrbg.—Shape roughly triangular, broadest in front, truncated behind; peristome very big and triangular, with well-developed membranellæ. Length 280 to 375 μ. Requires good aeration.[85]

Fellers and Allison (common). Francé. Fantham and Taylor, Fantham and Paterson; Losin-Losinsky (Turkestan, heavy steppe soil).

S. pustulata (O. F. M.) Ehrbg.—Smaller than *S. mytilus*; shape ovoid, slightly flattened, with the two ends equally rounded. Length 180 to 220 μ. Tolerant of carbon dioxide.[85]

Fellers and Allison (occasional); Yakimoff and Zérèn (very frequent, found in 10 out of 15 soils; size 45 to 114μ × 30 to 57μ).

Stylonychia sp.—? St Vincent (Cape Verde Island). Piettre and Souza, Taylor and Burns, Nowikoff.

In view of the abundance of these species in stagnant water, etc., their scarcity in soil is noteworthy.

Family (ii.) *Euplotina* (Ehrbg.) Stein.—*Small rigid ciliates, short and compact in shape and dorso-ventrally flattened; peristome with adoral row of membranellæ; ventral cirri much reduced; lateral cirri not in rows but confined to posterior region; 5 well-developed anal cirri; contractile vacuole single, near right posterior end; macronucleus a long curved band.*

Euplotes, Ehrbg.—Shape oval, with large triangular peristome reaching to the middle of the body.

E. carinata, Stokes.—Left-hand border extended in the middle to form a definite angle instead of a smooth curve; dorsal surface ridged; 7 frontal, 3 ventral, 5 anal, and 4 marginal cirri. Length up to 95μ. Egypt (2). Fellers and Allison (rare).

E. charon (O. F. M.).—Shape regular, oval, slightly narrower in front than behind; peristome rather narrow; dorsal furrows not very distinct; 10 fronto-ventral cirri on anterior half of ventral surface. Very tolerant of deficiency of oxygen[85]. Length 80μ. England (length 35 to 80μ), Mauritius. Wolff (field soils), Fellers and Allison (occasional) (Plate VI., Fig. 10).

E. harpa, Stein.—Elongated oval, nearly twice as long as broad, widest in front, with tooth-like process at anterior right-hand corner and two more on the anterior edge of the ventral surface. Seven frontal, 9 ventral, 5 anal, and 4 marginal cirri. Length about 170 μ.

Fantham and Taylor, Fantham and Paterson.

E. patella, Ehrbg.—Roughly oval, but left-hand side almost straight, right-hand side convex and oblique in front; 9 fronto-ventral, 5 anal and 4 marginal cirri, the posterior two marginal cirri being often branched; ventral surface with longitudinal ridges in neighbourhood of the anal cirri. Length 100 to 125 μ, breadth 60 to 75 μ. Food largely diatoms and other algæ.

Fantham and Taylor (twice only). Fantham and Paterson (once only).

Euplotes sp.—Lodge and Smith, Waksman.

Family (iii.) *Aspidiscina*, Stein.—*Like the preceding family but with peristome long and narrow, running along the left-hand side only. Seven fronto-ventral cirri and 5 anal cirri; no marginal cirri.*

Aspidisca, Ehrbg.—Characters as of family.

A. costata, Duj.—Shape oval, narrower in front, ventral surface plane; peristome with an extension which projects right over the right-hand margin of the animal towards the posterior end; 6 longitudinal furrows on dorsal surface. Length 30 to 40 μ.

Fellers and Allison (occasional), Fantham and Taylor (once only), Fantham and Paterson (several soils), Yakimoff and Zérèn (in 3 out of 15 soils).

A. lyncaster, Stein. — Ovate, left-hand border notched at anterior end and near posterior end so as to form two backwardly-directed processes. Length 56 to 70 μ.

Yakimoff and Zérèn (a single vegetable garden soil).

Aspidisca sp.—Nowikoff.

Phacodinium muscorum, Prowazek.[95]—Shape lenticular and laterally compressed; enclosed in a thick pellicle, which is extended on either side at the ventral edge to form projecting plates, one of which bears the peristomial membranellæ; mouth near posterior end; 6 longitudinal ridges with a row of about 20 cilia in each of the furrows, macronucleus elongated but shorter than in *Euplotes*. Length not stated (approximately 160 μ from Prowazek's diagram).

Francé (1921).

ORDER 5.—PERITRICHA. TYPICALLY SESSILE, OFTEN STALKED, CILIA ENTIRELY ABSENT EXCEPT FOR A RING OF ADORAL MEMBRANELLÆ, WHICH LEADS DOWN TO A VESTIBULE INTO WHICH THE PHARYNX AND CONTRACTILE VACUOLES OPEN, AND A POSTERIOR RING OF CILIA WHICH IS TEMPORARILY PRESENT IN MANY SPECIES.

Vorticella, Linn. — Cup- or bell-shaped with a contractile stalk; solitary; pharynx conspicuous.

V. microstoma, Ehrbg.—Shape ovate, broadest in middle and narrowing in region of peristome which is not everted and is about $\frac{1}{2}$ the maximum width of the body; cuticle with fine transverse striations. Length 60 to 100 μ (Plate VI., Fig. 11). A common soil form. Egypt (2), Nauru, Tristan da Cunha, Gough Island (3), St Helena, Spitsbergen (2),

Greenland, Argentine, Congo, Mauritius, England. Goodey (arable soils; old stored Rothamsted soil). Fellers and Allison (common), Nowikoff, Yakimoff and Zérèn (in 7 out of 15 soils; length 30 to 38 μ). Losin-Losinsky (Turkestan, heavy steppe soil).

V. striata, Duj. — Possibly only a variety of *V. microstoma* and distinguished from it solely by the more distinct transverse striations.

Fellers and Allison (one of the six commonest soil protozoa). As no other investigators have mentioned this species at all it is clear that the organism referred to is one that has been recorded by them under another name or names, almost certainly *V. microstoma.*

V. campanula, Ehrbg. — Fantham and Taylor, Fantham and Paterson. These authors mention no other species, so it is probable that this record also refers to *V. microstoma.*

V. citrina, Ehrbg.—Fellers and Allison (common).

V. globularia, O. F. M.—Fellers and Allison (occasional).

V. nebulifera, Ehrbg.—Nowikoff, Yakimoff and Zérèn (in one vegetable garden soil). Losin-Losinsky (Turkestan, heavy steppe soil).

V. putrina, O. F. M. — Fellers and Allison, Goodey.

Vorticella spp.—Emmerich, Leiningen and Leow (only in "Hochmoorboden"), Gainey, Jameson,[61] Koch (several different species; only in rich, *e.g.* greenhouse soils, not in field soils), Waksman, Taylor and Burns.

Epistylis coarctata, Clap. and Lach.—Like *Vorticella* but colonial; stalk not contractile and often dichotomously branched. Goodey (pasture soil).

Epistylis sp.—Goodey.

Cothurnia doliolum, Penard.—Solitary, surrounded by a test into which it can withdraw; very contractile; test attached by posterior end.

Francé.

Vaginicola terricola, Greef.—Like *Cothurnia* but flattened and with the test attached by its side (not by the posterior end).

Francé.

Key to the Identification of the Soil Ciliates.

In this case the most easily observed features are those which distinguish the orders and sub-orders of the class.

Sections A and B of the key accordingly enable these main groups to be distinguished, and refer to subsequent sections from which the genera in each group can be identified. As an additional help a classification based on the structure of the macronucleus is also included (Sections 1 to 6), as this feature can generally be easily observed either in the living organism or after killing with iodine solution or with acetic carmine.

Ciliata.

A. Cilia all alike—Simple, and Distributed Uniformly or in Longitudinal Rows.

(a) *No peristome.*

(i) Mouth terminal—Holotricha I. (7-13).

(ii) Mouth lateral or ventral—Holotricha II. (14-24).

(b) *Big peristome present with one or more large undulating membranes but no membranellæ.*
Mouth ventral—Holotricha III. (25-28).

B. Some or All of the Cilia fused together to form Membranellæ, Cirri, Etc.

(a) *No peristome.*
Holotricha IV.—*Mesodinium:* shape more or less spherical; cilia absent except for a ring of membranellæ in an anterior transverse groove; mouth at anterior pole (1).

(b) *Peristome bordered by row of membranellæ which do not form a closed ring* (29-39).
Heterotricha: cilia fine and uniform, generally arranged in longitudinal rows.
Hypotricha: no cilia on dorsal surface; ventral and marginal cilia fused together to form cirri the arrangement of which is characteristic of each genus.

(c) *Peristome bordered by a row of membranellæ which form a closed ring.*
(i) Free-swimming—Oligotricha (40).
(ii) Sessile—Peritricha (41, 42).

Macronucleus:—

(1) A single spherical or ellipsoidal mass.
Holotricha I.—
Holophrya (7, 12).
Urotricha (7, 11, 12, 13).
Enchelys (8).
Prorodon (7, 13).
Coleps (9, 10).
Holotricha II.—
Nassula (14, 21, 24).
Chilodon (15, 24).
Trochilia (15, 20, 23).
Uronema (14, 19, 22).
Cryptochilum (14, 19, 22).
Glaucoma (14, 22, 23).
Colpidium (14, 22, 23.)
Colpoda (16, 23).
Paramœcium (14, 23).

MACRONUCLEUS—*contd.*

(1) A single spherical or ellipsoidal mass—*contd.*

Holotricha III.—
Pleuronema (25, 27).
Cyclidium (25, 27).
Balantiophorus (25, 26, 28).
Anophrys (26, 28).

Holotricha IV.—
Mesodinium.

Heterotricha—
Blepharisma (32, 37).
Metopus (31, 37).
Metopides (31, 37).

Oligotricha—
Strombidium (40).
Halteria (40).

(2) Two spherical or ellipsoidal masses.

Holotricha I.—
Lacrymaria (8, 10).

Holotricha II.—
Amphileptus (17).
Lionotus (17, 20).

Holotricha III.—
Lembus (26, 27).

Hypotricha—
Stichotricha (32, 35, 37).
Uroleptus (most spp.), (3, 33, 35, 38, 39).
Gastrostyla—two or four (3, 30, 35, 38).
Gonostomum—nuclei rather elongated (31, 35, 37).
Oxytricha (31, 35, 37, 38).
Pleurotricha (31, 35, 38).
Stylonychia (31, 33, 34, 35, 37).

(3) More than two spherical or ellipsoidal masses.

Holotricha I.—
Chœnia—nuclei numerous (8, 10).

Holotricha II.—
Loxophyllum—numerous small ellipsoidal masses (18, 20).

MACRONUCLEUS—*contd.*

(3) More than two spherical or ellipsoidal masses—*contd.*

Hypotricha—

Urostyla—numerous small rounded masses difficult to see (30, 35, 38).

Uroleptus mobilis—six (33, 35, 39).

Onychodromus—four to eight (30, 35, 37).

Gastrostyla—two or four (2, 30, 35, 38).

(4) Straight transverse band broader at ends.

Oligotricha—

Strombilidium (40).

(5) Long curved band.

Holotricha I.—

Spathidium (8, 10).

Hypotricha—

Euplotes (30, 36).

Aspidisca (30, 36).

Phacodinium—nucleus shorter than in *Euplotes* (30, 36).

Peritricha—

Vorticella (41).

Epistylis (41).

Cothurnia (42).

Vaginicola (42).

(6) Moniliform.

Holotricha II.—

Dileptus (17).

Heterotricha—

Spirostomum — the macronucleus in this genus is variable, being a single ellipsoidal mass in *S. teres*. This species, however, has not been recorded from the soil (31, 36).

Condylostoma (29, 36).

HOLOTRICHA I.:—

(7) Shape: spherical to ovoid or ellipsoidal.

Holophrya—sometimes rather elongated (1, 12).

Urotricha (1, 11, 12, 13).

Prorodon—mouth sometimes sub-terminal (1, 13).

HOLOTRICHA I.—*contd.*

(8) Shape: cylindrical or elongated.

Enchelys—anterior end somewhat tapering and truncated (1).

Spathidium—with short neck, squarely truncated in front (5, 10).

Lacrymaria—flask-shaped, with long neck, very flexible; mouth situated on small conical projection at anterior end (2, 10).

Choenia—with neck, flexible (3, 10).

(9) Shape: barrel-shaped with firm carapace.

Coleps (1, 10).

(10) Cilia: ring of cilia around mouth rather longer than the others.

Spathidium (5, 8).
Lacrymaria (2, 8).
Choenia (3, 8).
Coleps (1, 9).

(11) Cilia: one or more long caudal cilia.

Urotricha (1, 7, 12, 13).

(12) Pharynx present: simple.

Holophrya (1, 7).
Urotricha spp. (1, 7, 11).

(13) Pharynx present: surrounded by rods.

Urotricha farcta (1, 7, 11).
Prorodon (1, 7).

HOLOTRICHA II.:—

(14) Shape: ovoid or ellipsoidal.

Nassula—hind end rather broader than front end (1, 21, 24).

Uronema—slightly compressed laterally (1, 19, 22).

Cryptochilum—slightly compressed laterally (1, 19, 22).

Glaucoma—slightly compressed dorsoventrally (1, 22, 23).

Colpidium—slightly compressed dorsoventrally; rather elongated (1, 22, 23).

Paramœcium—rather elongated; mouth at base of an oblique groove (1, 23).

HOLOTRICHA II.—*contd.*

(15) Shape: oval, strongly flattened and asymmetrical.
Chilodon (1, 24).
Trochilia (1, 20, 23).

(16) Shape: more or less bean-shaped; sometimes pointed in front; mouth in a deep ventral notch.
Colpoda (1, 23).

(17) Shape: elongated.
Amphileptus: anterior end forming a trunk, very flexible; mouth in a shallow antero-lateral groove (2)
Lionotus—flattened, anterior end narrow; mouth in a shallow, antero-lateral groove (2, 20).
Dileptus—anterior end forming a trunk, very flexible; mouth at base of trunk (6).

(18) Shape: leaf-like.
Loxophyllum—very flexible and contractile; mouth in a shallow, antero-lateral groove (3, 20).

(19) Ciliation: with long caudal cilium.
Uronema (1, 14, 22).
Cryptochilum—caudal cilium rather oblique (1, 14, 22).

(20) Ciliation: cilia on one side of body only.
Lionotus—longer cilia along side of mouth (2, 17).
Loxophyllum (3, 18).
Trochilia—cilia limited to a longitudinal ventral band (1, 15, 23).

(21) Ciliation: with an adoral row of stronger cilia.
Nassula (1, 14, 24).

(22) Ciliation: mouth with a small undulating membrane.
Uronema (1, 14, 19).
Cryptochilum (1, 14, 19).
Glaucoma (1, 14, 23).
Colpidium (1, 14, 23).

(23) Pharynx present: simple.
Trochilia—pharynx long (1, 15, 20).
Glaucoma—pharynx short and shallow (1, 14, 22).
Colpidium—pharynx short (1, 14, 22).
Colpoda—pharynx short (1, 16).
Paramœcium—pharynx short (1, 14).

HOLOTRICHA II.—*contd.*

(24) Pharynx present with rods.

Nassula—pharynx long (1, 14, 21).
Chilodon—pharynx long (1, 15).

HOLOTRICHA III.:—

(25) Shape: ovoid to ellipsoidal.

Pleuronema (1, 27).
Cyclidium (1, 27).
Balantiophorus minutus (1, 28).

(26) Shape: elongated.

Balantiophorus elongatus (1, 28).
Lembus—anterior end a narrow trunk: very flexible (2, 27).
Anophrys—anterior end tapering but not so narrow as in *Lembus* (1, 28).

(27) Undulating membrane very long: mouth near posterior end of body.

Pleuronema (1, 25).
Cyclidium—with long caudal cilium (1, 25).
Lembus—mouth at or just behind middle of body (2, 26).

(28) Undulating membrane short: mouth near anterior end of body.

Balantiophorus (1, 25, 26).
Anophrys—mouth just in front of middle of body (1, 26).

HETEROTRICHA AND HYPOTRICHA:—

(29) Shape: ovoid to ellipsoidal.

Condylostoma—slightly flattened dorsoventrally (6, 36).

(30) Shape: oval and flattened.

Euplotes—quite rigid (5, 36).
Aspidisca ,, (5, 36).
Phacodinium ,, (5, 36).
Urostyla—no carapace, slightly flexible (3, 35, 38).
Onychodromus—no carapace, not flexible (3, 35, 37).
Gastrostyla steinii—no carapace, slightly flexible (2, 3, 35, 38).

HETEROTRICHA AND HYPOTRICHA—*contd.*

(31) Shape: elongated, ends about equally rounded.

Metopus—anterior end twisted, very contractile (1, 37).

Metopides—anterior end twisted, shape persistent (1, 37).

Spirostomum—very narrow, vermiform, flexible, and contractile (6, 36).

Gonostomum—very flexible (2, 35, 37).

Oxytricha—very flexible, ventral surface flattened (2, 35, 37, 38).

Pleurotricha—not flexible, ventral surface flattened (2, 35, 38).

Stylonychia pustulata—not flexible, ventral surface flattened (2, 34, 35, 37).

(32) Shape: elongated, tapering at anterior end.

Blepharisma—not flexible, laterally compressed (1, 37).

Stichotricha—anterior end forming a narrow contractile trunk (2, 35, 37).

(33) Shape: elongated, tapering at posterior end.

Uroleptus—most species have a distinct tail; very flexible (2, 3, 35, 38, 39).

Stylonychia mytilus—anterior end very broad, posterior end narrower; ventral surface flattened (2, 31, 34, 35, 37).

(34) With three long caudal bristles.

Stylonychia (2, 31, 33, 35, 37).

(35) Arrangement of ventral cirri—

Five or more longitudinal rows.

Urostyla (3, 30, 38).

Three or four longitudinal rows.

Onychodromus (3, 30, 37).

Two or more longitudinal rows with an additional median group.

Pleurotricha (2, 31, 38).

Two longitudinal rows: anal cirri absent.

Uroleptus (2, 3, 33, 38, 39).

One longitudinal row and some scattered cirri.

Gastrostyla (2, 3, 30, 38).

One oblique row.

Stichotricha (2, 32, 37).

HETEROTRICHA AND HYPOTRICHA—*contd.*

(35) Arrangement of ventral cirri—*contd.*
Five or six cirri in an oblique row.
Gonostomum (2, 31, 37).
Five ventral cirri not arranged in a row.
Oxytricha (2, 31, 37, 38).
Five ventral cirri not arranged in a row.
Stylonychia (2, 31, 33, 34, 37).

(36) Peristome extending slightly beyond middle of body.
Spirostomum (6, 31).
Condylostoma (6, 29).
Euplotes – peristome broad (5, 30).
Aspidisca—peristome narrow (5, 30).
Phacodinium (5, 30).

(37) Peristome extending to middle of body.
Blepharisma (1, 32).
Metopus (1, 31).
Metopides (1, 31).
Stichotricha (2, 32, 35).
Onychodromus (3, 30, 35).
Gonostomum—peristome runs parallel to long axis of body for the greater part of its length and then turns sharply inwards (2, 31, 35).
Oxytricha bifaria (2, 31, 35, 38).
Stylonychia—peristome very broad in *S. mytilus* (2, 31, 33, 34, 35).

(38) Peristome extending about one-third of the body-length.
Urostyla—peristome very broad (3, 30, 35).
Uroleptus musculus (2, 33, 35, 39).
Gastrostyla (2, 3, 30, 35).
Oxytricha (2, 31, 35, 37).
Pleurotricha (2, 31, 35).

(39) Peristome extending less than one-third of the body-length.
Uroleptus (most species), (2, 3, 33, 35, 38).

OLIGOTRICHA :—

(40) *Strombilidium*—pyriform, body cilia absent (4).
Strombidium — spherical to ovoid, few scattered cilia on ventral surface (1).

OLIGOTRICHA—*contd.*

Halteria—spherical, with equatorial row of long springing bristles (1).

PERITRICHA:—

(41) Naked.

Vorticella—solitary, stalk contractile (5).

Epistylis—colonial, stalk branched and not contractile (5).

(42) Enclosed in a test.

Cothurnia—test attached to support at posterior end (5).

Vaginicola—test with a flattened side which lies against the support (5).

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EXPLANATION OF PLATES

In Plates I., III., and IV., the drawings are made from either living or fixed and stained soil specimens; Plates II., V., and VI. are redrawn from the descriptions and figures given by the various authorities who have described the species.

It will be noticed that in many of the figures on these plates the magnifications given do not agree with the dimensions given in the text for these organisms, the former dimensions being those given for the originals of which these drawings are copies, while the latter are from measurements of the organisms in soil cultures wherever possible. In such cases the soil forms are invariably much smaller than those given by the authorities. The significance of *size* in the protozoa is not at present sufficiently well understood for any discussion of this rather striking fact to be very profitable.

The magnification and methods of staining and fixing are noted in each case; the following abbreviations are used. Sch. = Schaudinn's sublimate-alcohol acetic mixture: Bou. = Bouin's picric alcohol mixture: H.I.H. = Heidenhain's iron-alum hæmatoxylin: B.R. = Bordeaux Red: Hæm. = Dobell's hæmatein: Eo = Eosin.

PLATE I.

Cysts of Common Soil Protozoa—Drawings from Life.

FIG.

1, 2 *Cercomonas longicauda.* × 2500.

3 „ *crassicauda.* × 2000.

4, 5 *Cercobodo vibrans.* × 2500.

6, 7 *Heteromita globosa* with and without pores. × 2500.

8 *Sainouron mikroteron.* × 2500.

9-11 *Tetramitus spiralis*, 8-sided cyst in three different positions. × 2500.

12 *Tetramitus spiralis*, 6-sided cyst, free-hand drawing. × 2500.

13-18 *Oikomonas termo*, successive stages of cyst formation and mature cysts; Figs. 13-15 free-hand drawings. × 2500.

PLATE I.—*contd.*

FIG.

19 *Allantion tachyploon.* × 2500.

20 *Hartmanella hyalina.* × 2500.

21 *Nægleria gruberi.* × 1500.

22 *Amœba* sp. (? *A. albida*). × 2500.

23 *Colpoda steinii.* × 2500.

24 „ *maupasii.* × 2500.

25 *Gonostomum affine.* × 2500.

NOTE.—Owing to the method of drawing, the highly refringent globules in the cysts of *Heteromita globosa* and of *Allantion tachyploon* appear in these figures as hollow rings (figs. 6, 7, 19).

PLATE II.

FIG.

1 *Mastigamœba limax*, Moroff, after Moroff. × 2000.

2 *Cercomonas crassicauda* (Alexeieff) Lemmermann, after Dobell and O'Connor. × 2000.

3 *Cercomonas crassicauda*, amœboid form after Dobell and O'Connor. × 2000.

4 *Cercobodo agilis*, Moroff, after Moroff. × 2000.

5, 6 *Oikomonas termo* (Ehrbg.) Martin, after Martin. × 2000.

7, 8 *Bodo saltans*, Ehrbg., after Goodey. Fig. 7 in early stage of division.

9 *Bodo edax*, Klebs, after Klebs. × 2000. (This species is typically narrower than the specimen figured here.)

10 *Monosiga ovata*, Kent, after Kent. × 2000. (The stalk is generally not present, and only the two side lines of the "collar" can be seen with the ordinary microscopic methods.)

11 *Phyllomitus undulans*, Stein, after Stein. × 2000.

12 *Tetramitus rostratus*, Perty, after Stein. × 650.

13 *Entosiphon sulcatum* (Duj.) Stein, after Stein. × 650.

14 *Scytomonas pusilla*, Stein, after Dobell and O'Connor. × 2000.

PLATE III.

Active Soil Protozoa—mostly from Stained and Fixed Specimens.

1 *Cercobodo vibrans*, free-swimming form. Bou., H.I.H., B.R. × 3100.

2 *Cercobodo vibrans*, partly amœboid. Bou., H.I.H., B.R. × 3100.

3 *Cercobodo vibrans*, completely amœboid. Bou., Hæm. × 4100.

4, 5 *Helkesimastix fæcicola.* Sch., H.I.H. × 4100.

PLATE III.—*contd.*

FIG.

6 *Phalansterium solitarium*, living unstained, sessile form enclosed in mucilaginous capsule. × 2500.

7 *Phalansterium solitarium*, fixed and stained specimen (in this the collar has closed round the base of the flagellum). Bou., H.I.H., B.R. × 2500.

8 *Phalansterium solitarium*, free-swimming form (in this condition the collar is very rarely visible—it is generally entirely absorbed into the body as in this figure). Bou., H.I.H., B.R. × 2650. In Figs. 7 and 8 only the basal part of the flagellum is drawn.

9 *Sainouron mikroteron*, normal active. Sch., H.I.H. × 2050.

10, 11 *Sainouron mikroteron*, conjugation. Sch., H.I.H. × 4100.

12, 13 *Colponema symmetrica* (Fig. 13 is partly side view showing the longitudinal groove which is not visible in fixed specimens in surface view. Sch., H.I.H. × 4100.

14 *Allantion tachyploon*, living unstained. × 2500.

15 *Allas diplophysa*, living unstained. × 2500.

PLATE IV.

1-9 *Allas diplophysa*, nuclear division. Bou., Hæm. × 4100.

10 *Nuclearia* sp., living specimen. × 2500.

11 ,, fixed and stained. Bou., H.I.H., Eo. × 3000.

PLATE V.

1 *Biomyxa vagans*, Leidy, after Cash. × 300.

2 *Amœba diploidea*, Hartmann and Nägler, after Hartmann and Nägler. × 900.

3 *Nægleria gruberi* (Schardinger) Wilson, after Wilson. × 1000.

4 *Nægleria gruberi*, flagellate form, after Wilson. × 1000.

5 *Lecythium hyalinum* (Ehrbg.) Hertwig and Lesser (= *Chlamydophrys stercorea*, Cienk.), after Cash. × 300.

6 *Centropyxis lævigata*, Penard, after Cash, oral view. × 300.

7 *Centropyxis lævigata*, Penard, after Cash, side view. × 300.

8, 9 *Difflugia constricta* (Ehrbg.) Leidy, after Leidy. × 300.

10, 11 *Trinema enchelys* (Ehrbg.) Leidy, after Cash, oral and side views. × 300.

12 *Euglypha tuberculata*, Duj., after Cash. × 300.

13 *Nebela collaris* (Ehrbg.) Leidy, after Cash. × 300.

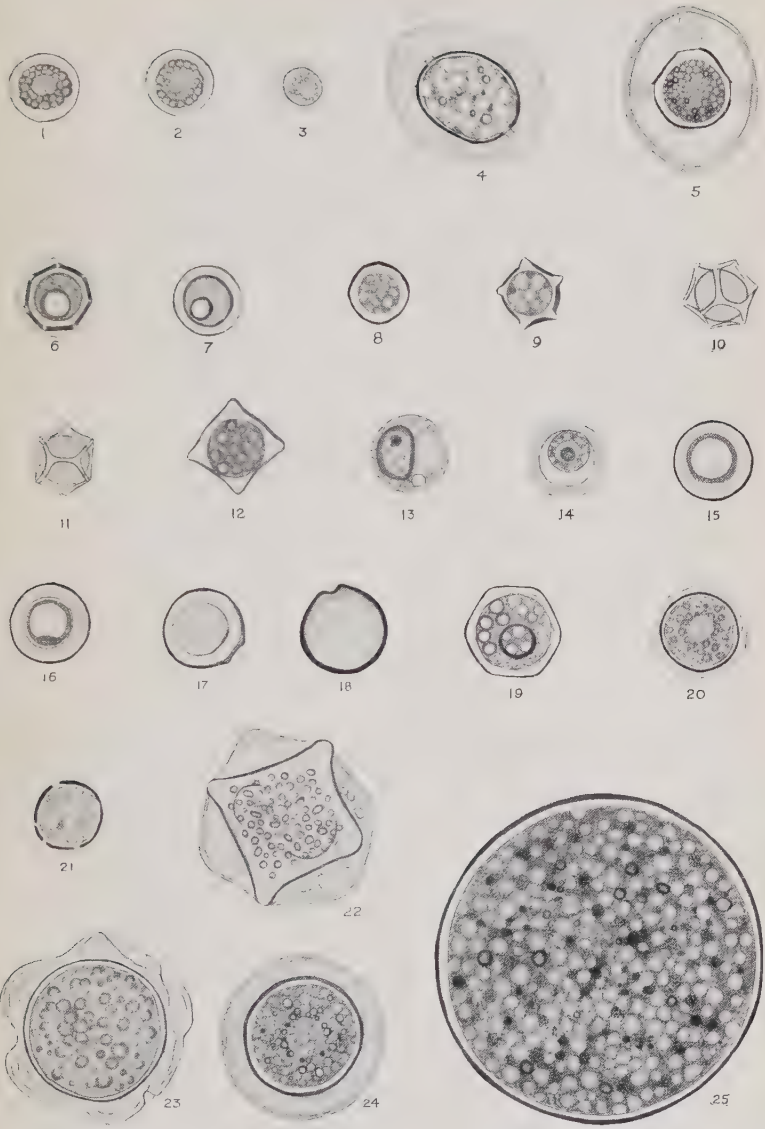
14 *Quadrula irregularis*, Archer, after Cash. × 600.

PLATE VI.

FIG.

1 *Colpoda cucullus* (O. F. M.), after Enriques. × 250.
2 „ *maupasii*, Enriques, after Enriques. × 330.
3 „ *steinii*, after Enriques. × 330.
4 *Colpidium colpoda*, Stein, after Schewiakoff. × 530.
5 *Chilodon cucullulus* (O. F. M.), after Stein. × 250.
6 *Cyclidium glaucoma* (O. F. M.), after Schewiakoff. × 500.
7 *Balantiophorus elongatus*, Schewiakoff, after Schewiakoff. × 500.
8 *Glaucoma scintillans*, Ehrbg., after Schewiakoff. × 350.
9 *Halteria grandinella* (O. F. M.), after Conn. × 500.
10 *Euplotes charon* (O. F. M.), after Stein. × 500.
11 *Vorticella microstoma*, Ehrbg., after Kent. × 250.
12 *Pleurotricha lanceolata*, Ehrbg., after Stein. × 500.
13 *Uroleptus musculus*, Ehrbg., after Stein. × 500.
14 *Oxytricha pellionella* (O. F. M.), after Stein. × 500.
15 *Gonostomum affine* (Stein), after Stein. × 500.

PLATE I.



Day & Night Teller ®

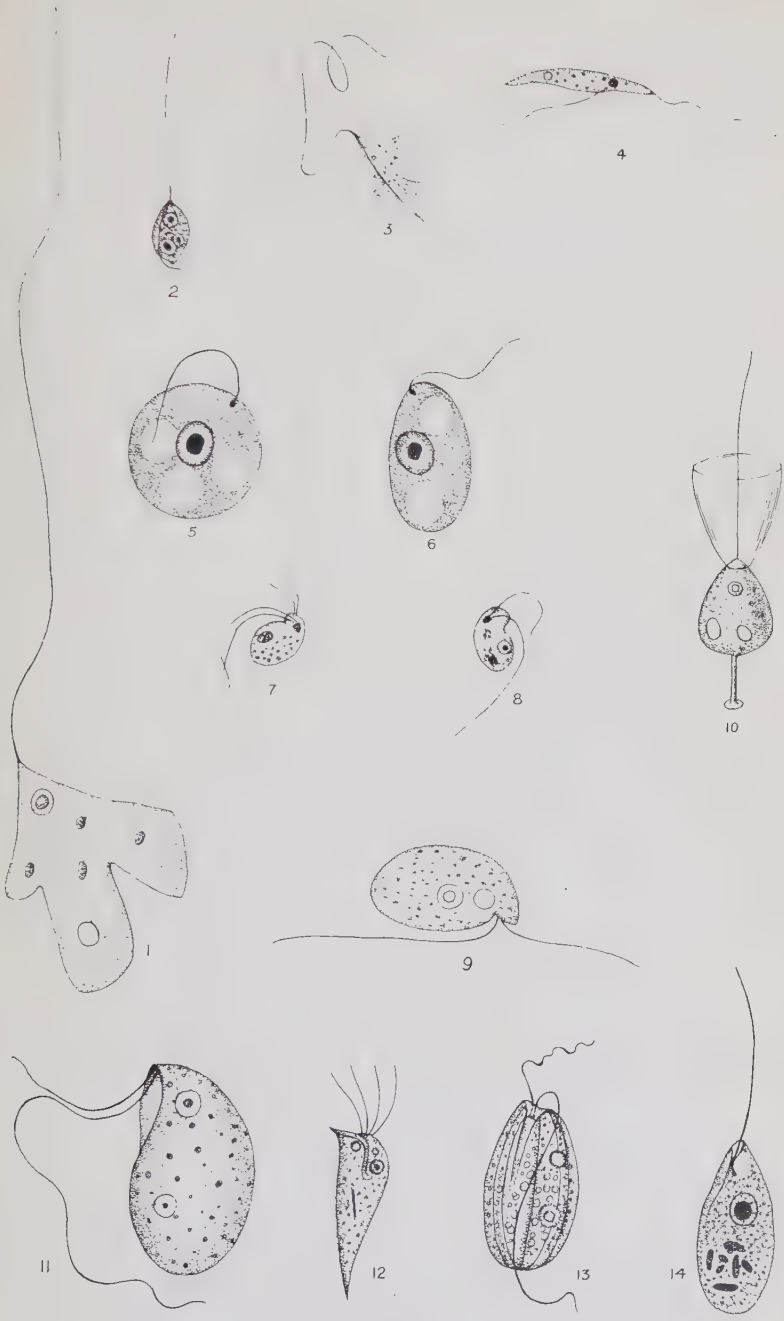


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PLATE IV.

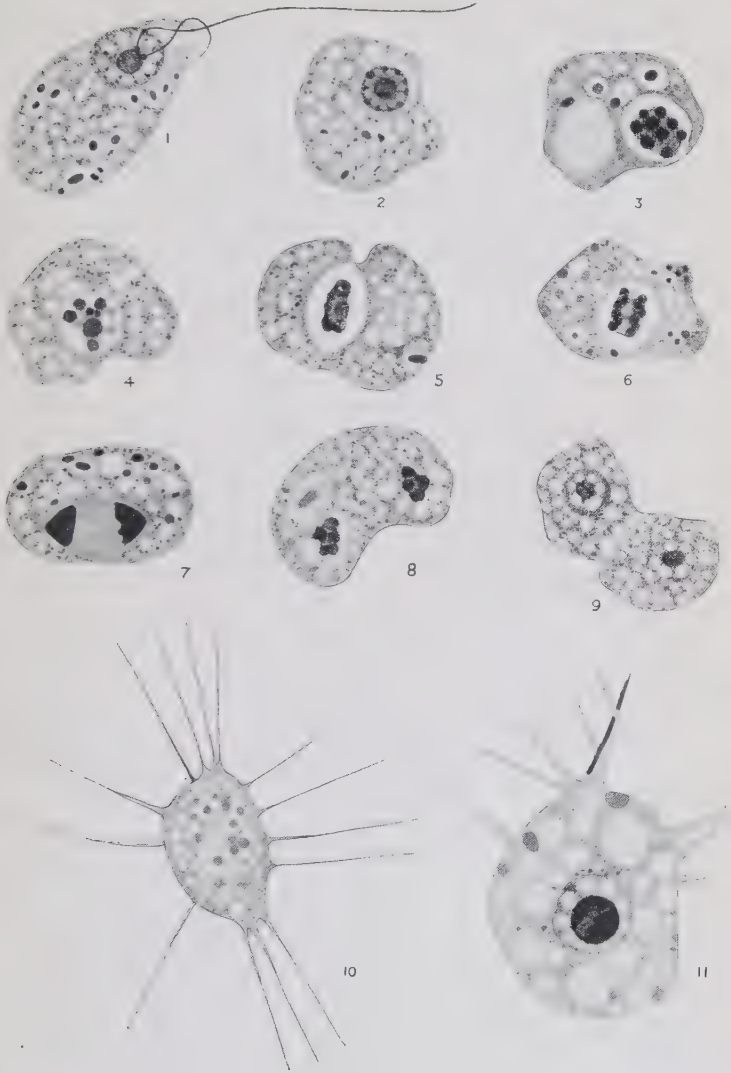

PLATE V.

PLATE VI.

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CHARTS

LIST OF PROTOZOA, SHOWING THEIR OCCURRENCE IN THE SOIL SAMPLES EXAMINED

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